VOL. 43 MAY 1916 NO. 5

JUN 1916
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BULLETIN

OF THE

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PUBLISHED FOR THE CLUB
THE NEW ERA PRINTING COMPANY
LANCASTER, PA.

THE TORREY BOTANICAL CLUB

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Bulletin. Monthly, established 1870. Price, $3.00 a year; single numbers 30 cents. Of former volumes, only 24–39 can be supplied separately; certain numbers of other volumes are available, but the entire stock of some numbers has been reserved for the completion of sets. Manuscripts intended for publication in the BULLETIN should be addressed to the Editor, Osborn Botanical Laboratory, Yale University, New Haven, Connecticut.

Torreya. Monthly, established 1901. Price, $1.00 a year. Manuscripts intended for publication in TORREYA should be addressed to Norman Taylor, Editor, Brooklyn Botanic Garden, Brooklyn, N. Y.

Memoirs. Occasional, established 1889. (See last pages of cover.)

Preliminary Catalogue of Anthophyta and Pteridophyta within 100 miles of New York City, 1888. Price, $1.00

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200 copies	1.70	2.35	2.90	3.75	4.35	4.70

Covers: 25 for 75 cents, additional covers 1 cent each.

Plates for reprints, 40 cents each per 100.

Vol. 43 No. 5

BULLETIN

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TORREY BOTANICAL CLUB

MAY, 1916

The origin of new varieties of Nephrolepis by orthogenetic saltation
I. Progressive variations

R. C. BENEDICT

(WITH PLATES 10–15)

A. INTRODUCTION

1. *Definition and scope of paper*

The title, "The origin of new varieties in *Nephrolepis* by orthogenetic saltation," was selected to emphasize two points: first, that the variations to be described are discontinuous and of considerable magnitude, *i.e.* jumps or saltations; second, that these variations occur in definite series along a few limited lines, *i.e.* they are orthogenetic. I purposely beg the question as to whether they are mutations or not because I do not know. The exact application of the term, mutation, seems at present to be in a state of some uncertainty, and in any event, there may be considerable question about classifying these vegetative fern sports in the same category with the forms of *Oenothera*, among which, surely, orthodox mutations must exist.

Nephrolepis is a genus of tropical ferns, several species of which have been cultivated. Nearly all these species have shown some variation under cultivation, but one of them, *N. exaltata*, through its variety, the so-called "Boston fern," *N. exaltata bostoniensis*, has been especially prolific of new forms. From this variety there have arisen in about fifteen years at least sixty

[The BULLETIN for April (43: 169–206. *pl.* 7–9) was issued May 20, 1916.]

named horticultural forms besides a probably equally large number which have never gained horticultural recognition. The present account is concerned only with a portion of these Boston fern varieties, the basis of selection being indicated below.

Reproduction in the Boston fern and its varieties, as indeed in the varieties of the other species of *Nephrolepis*, is almost exclusively vegetative. The varieties with a few possible exceptions have arisen strictly by bud variation, the explanation being found in the fact that almost all the forms, the wild species being excepted, produce imperfect sori with mostly abortive sporangia. As indicated, there are a few varieties reputed to have been raised from spores and there is nothing impossible in this connection, but there is also no question that the great majority of forms have developed from bud sports. Their study is therefore untroubled by questions of pure line or hybridization, nor does it readily allow these valuable analytical methods of attack, but calls mainly for an accurate determination of the origin and parentage of each form and an adequate description of its characters.

The large number of varieties mentioned includes a multiplicity of forms, some of which have arisen by progressive, some by regressive, variation. A complete description of all these at present would involve considerable difficulties in the way of preparation and presentation. The scope of this paper is therefore limited to deal mainly with the more pronounced lines of progressive variation. The terms "progressive," "regressive," and "reversion," are used here with only their ordinary non-technical connotation. Progressive variations as understood are those which show less resemblance to var. *bostoniensis* than do their parent forms. It must be understood here that the variations from var. *bostoniensis* include series of forms with as many as six successive intensifications of a given character by which the first of the series diverged from var. *bostoniensis*. Such a series is considered progressive (see PLATE 10). Regressive variations or reversions, on the other hand, are understood to be those which show something of a return in characters toward var. *bostoniensis*. This classification is largely one of convenience, and the separation of the two types of forms may not always be justified as made. It will, however, furnish a good basis for a description and discussion of these forms.

As preliminary to such description, it will be appropriate to consider some of the significant features of these variations, and to compare them with other variations of possibly similar nature. This discussion will be dealt with under two headings: viz., Earlier studies of orthogenesis; Conditions under which *Nephrolepis* varieties have originated.

2. *Earlier studies of orthogenesis*

The term "orthogenesis" was proposed by Haacke to characterize what the zoölogist, Eimer, had been calling "bestimmt gerichtete Entwicklung," *i.e.* "definitely directed evolution" as translated by T. J. McCormack.* It appears that the botanist, Nägeli, had expressed views similar to those of Eimer at a somewhat earlier date. The evidence upon which these writers built their conclusions was systematic, and dealt with groups of living species showing close relationship. An orthogenetic series for Eimer was, for example, a group of related butterflies, the relationships between which was traced by gradations in the markings which varied from one extreme to another, but were connected by intervening forms. Evolution was postulated as progressive in one direction or the other.

Later writers, such as Cope, Hyatt, Grabau, and Osborn, have considered orthogenesis in connection with groups of organisms in geologic series. Grabau, for example, has illustrated orthogenesis in gastropods† by series of fossils from successive strata, which show gradual but definite progressive variation in the sculpture of the shells.

A third line of orthogenetic study is illustrated by Coulter's recent discussion of orthogenesis in gymnosperms.‡ This, of course, is similar to that of Grabau, Hyatt, etc., in that it deals with extinct forms, but differs in being applied to a much longer period of variation and to less closely related forms, and it differs further in that it deals with the evolution of *organs* as such, the egg, proembryo, seed, etc., rather than with the phylogeny of *organisms*.

* Eimer. On orthogenesis. Chicago. 1898.

† Studies in Gastropoda III. Am. Nat. 41: 607–651. 1907.

‡ Science II. 42: 859–863. 1915.

The conclusions reached by the writers specified above are like those of any similar morphologic or systematic research, but differ in the use of the term "orthogenesis," instead of "tendency to vary," "trends of variation," or some similar expression. This difference is of interest, however, because it lays emphasis on the belief that the evolution of the present-day organic world has not been by chance fluctuation, but has proceeded in an orderly fashion in a law-conforming way. According to orthogenetic theory, evolution proceeds, at least in part, by the progressive intensification of characters in any series of forms, regardless of considerations of adaptation or utility. In the long run, of course, only such forms as possess useful characters will survive.

In the present case, the lines of variation do not appear to be in the interests of utility. The new forms produced are not as adaptable to natural conditions as the original species from which they all originated. Proof of this is found in the fact that the various new varieties are, in general, more difficult of cultivation than the original form, and further proof is contained in the fact that none of the varieties of *N. exaltata bostoniensis* have been found wild in the tropics. It may appear then that these fern varieties, produced so artificially and unnaturally, are poor forms to cite as illustrations of orthogenesis. This would be true were it not for the fact that the same types of variation appear everywhere among ferns as distinctive of recognized species or even genera. That is, fern species *have* differentiated naturally by the same manner and degree of variation as is shown by these horticultural varieties. On this basis, these Boston fern sports may be considered as unsuccessful variations, either premature or normal, perhaps called forth or at least perpetuated by the unusual cultural conditions. Like wild forms in other genera in the degree of their variation, they are unlike them in having developed no means of maintaining themselves under natural conditions, and if put to the test of competition, would soon be disposed of by natural selection. They may be said to indicate potentialities of variation in *Nephrolepis*. It is worth while noting that variations of similar type *but of spore origin*, have appeared in other fern genera, notably *Polypodium* and *Polystichum*.

3. *Conditions under which Nephrolepis varieties have originated*

It is suggested in the preceding paragraph that cultural conditions may be responsible in some degree for the development or preservation of so many new varieties. Two points are of special interest in connection with the cultural conditions: first, the fact that these are probably generally the optimum for these ferns; second, the very large numbers of individual plants raised each year.

For soil, the florist uses a good loam or leaf mould with at least one half to equal amounts of rotted manure. In one case the mixture used consists of one part sand to five parts rotted manure, leaf mould, and humus. New plants are propagated from stock plants which are planted out in long benches in shallow soil. A single stock plant may produce nearly one hundred runners, as the young plants are called, in a single year. These new plants develop from slender stolons which spring from the parent plant close to or connected with the leaf bases, and penetrate the soil in all directions. Each runner may produce a considerable number of buds as well as roots. It is worthy of present note that these stolons serve not only for reproduction but also as agents in the nourishment of the parent plant, at least until the secondary plants have attained some size. The main point to be noted in connection with the methods of propagation aside from the quality of the soil, etc., is the freedom of growth which is given the stock plants and their progeny in the early stages. The plants after potting are sometimes further fed with liquid fertilizer of some sort. They are grown in low-roofed houses with absence of draft, and usually with no other kinds of plants which might desire slightly different conditions. If variation is in any way connected with vigorous growth, there is every reason why these ferns should vary.

With respect to the number of plants grown per annum, it is hard to estimate in what will appear a conservative manner. I have talked with two growers who claimed to sell three and four hundred thousand small plants every year and there seemed to be no reason why they should be exaggerating. There are undoubtedly half a dozen florists in the eastern states who raise over one hundred thousand plants each year, and a larger number who produce fifty thousand. The number who grow fifteen to twenty thousand

is of course much larger still. Some deduction from the total thus indicated must be made in connection with smaller growers because of the fact that many buy part or all of their stock of ferns each year as small plants to raise to larger sizes. A single plant may thus be sold twice at wholesale, and once at retail, and the non-growing jobber may come in to make a third wholesale transfer. Taking everything into consideration, however, it seems safe to put the total number of plants raised every twelve months at not less than one million, and probably nearer two. As will readily be seen, this immense number offers large possibilities for the occurrence of variation.

A third factor connected with the selection and preservation of new varieties of these ferns is found in the fact that some of these varieties have been the means of large profits to their producers. The first good two-pinnate sport of var. *bostoniensis* created a furor in the florist trade, and was awarded gold medals and other insignia which no other new plant has ever received. The regular price for a small plant of a standard variety from a two and a half inch pot is five cents in hundred lots. New forms of merit now sell at introduction for twenty-five cents apiece, and some new forms have sold as high as one dollar per plant. In the past this has led to the exercise of great watchfulness for new forms of possible merit, and has thus aided in the discovery and development of new varieties. So many forms have now been developed, however, that there appears to be a reaction from the interest in new forms.

The figure as to the number of plants grown per year suggests the possibility of determining an approximate coefficient of variation, but this seems to be an almost impossible problem. For one variety about which I have made inquiry, the number indicated is at least one in three thousand. For another variety which is appearing rather frequently in different establishments at present, the coefficient is undoubtedly higher, perhaps one in one thousand. For yet another variety a figure of one in a million is probably too high an estimate. It should be added that these figures are for progressive variations only. Reversions or regressive variations appear much more frequently as a rule.

Two conclusions are evident from the foregoing: (1) the coefficient of variation differs with different varieties; (2) the coefficient of variation is never high for progressive variations.

4. *Methods of study*

One method of study of the Boston fern problem is indicated by the above facts as almost obligatory, viz., frequent visits to florists' establishments for purposes of observation. During the last two years I have visited nearly all the leading fern growers in the eastern states. Visits have been made to the greenhouses of the growers in Massachusetts, New York, New Jersey, Pennsylvania, and Ohio, who have produced practically all the new forms of *Nephrolepis* raised east of the Mississippi. These visits are being continued, and arrangements have been made for experimental work through the coöperation of some of the growers.

A second method of study has been connected with the assembling of a living collection of all obtainable varieties of these ferns at the Brooklyn Botanic Garden. These collections now number at least seventy-five varieties, nearly all obtained directly from their original producers, and orders are now in the hands of English and French growers for foreign varieties which will raise the total number to over one hundred. Requests have also been sent to a number of stations in the tropics for the collection of wild forms with a view to obtain a good representation of both horticultural and natural forms.

Still a third method which is really a combination of the other two has consisted in the introduction to florists all over the country of varieties with which they were not familiar. A large number of small plants have been sent out in this way. The benefit to the investigation will come in connection with future visits when a much larger number of varieties will be available for observation. A considerable number of new forms have also been obtained in this way by exchange.

It will be noted that there is little opportunity for the experimental production of new progressive variations in connection with the Botanic Garden collection. Not enough plants can be grown. In the florists' establishments, the number of plants may be large enough but it is not always possible to control all conditions or to find sufficient time for regular and thorough observation.

The greatest difficulty which inheres in the study of the known forms of these ferns is connected with the possible inaccuracy of the growers. For the facts as to the origin and parentage of each

variety it is necessary to rely almost wholly on the statement of the florist who produced it. With every desire for accuracy, the grower may easily be mistaken with respect to the relationship of any given form, even if it has been under his eye since its first appearance. Plants of various forms are often grown together in stock beds, and the stolons may spread two or three feet in all directions with consequent mixing of the runners. When a form is discovered by one florist and sold for development and introduction to another, there is still greater chance for inaccuracy.

In general, however, there is every reason for believing that the statements which follow regarding the origin and relationship of the varieties are in the main accurate. Many of them, nearly all, in fact, are established beyond the possibility of any reasonable doubt. A few are definitely indicated as open to possible question.

It is a pleasure to acknowledge indebtedness to the numerous florists who have contributed to the living collections which have been built up almost exclusively by their gifts of plants. A nearly complete list of the contributing florists is given at the end of this paper in connection with an index of the varieties. To Mr. W. R. Maxon, of the United States National Museum, my thanks are due for valuable information regarding his collections and observations of these ferns in the tropics. For the opportunities at the Brooklyn Botanic Garden, without which complete data could not have been accumulated, I am glad to make grateful acknowledgment to Dr. C. Stuart Gager, the director. To Dr. O. E. White of the same institution I am indebted for a reading of my manuscript and a number of suggestions. Finally the study has been aided by a grant of one hundred dollars from the American Association for the Advancement of Science, made at the Columbus meeting, which will be applied to the expenses incident to the visits to florists. Only a small part of this has so far been used, most of the visits to date having been made at private expense.

B. ORIGIN AND DESCRIPTION OF THE VARIETIES IN NEPHROLEPIS

1. *N. exaltata and N. exaltata bostoniensis*

Nephrolepis exaltata, or rather its variety *bostoniensis*, has been named as the form from which the variations under consideration have all originated. As already noted, a number of other species in the genus have also given rise under horticultural conditions to variations similar to those of *N. exaltata*, but none of the other species has received as extensive cultivation, and there has, therefore, been less opportunity for variation. It may be noted here that all the wild species forms of *Nephrolepis* are once-pinnate. This is significant in consideration of the fact that among the varieties of *N. exaltata bostoniensis* are two-, three-, four-, and even five-pinnate forms. So far as I have been able to discover, only two partial aberrations from the once-pinnate type have been found wild; one, *N. biserrata* ("*davallioides*") *furcans*, with dichotomously divided pinnae, the so-called "fish-tail" form of the florists (see PLATE 12, FIG. 3, for illustration of this type of variation in the variety *falcata*); and the other, the anomalous form known as *N. Duffii* from New Zealand, referred by Goebel to *N. cordifolia* as a variety.

N. exaltata is a species of common and general occurrence in tropical America, and of somewhat scattered distribution in the Old World tropics. As I have it from Porto Rico, it appears as a plant with narrow erect leaves with sharply acute pinnae (PLATE 13, FIG. 1), well deserving its common name of "sword fern."* The sori are well developed and large with many fully formed sporangia. Presumably this form has been in cultivation in America for over fifty years, although the source and exact character of the original introduction are uncertain. It seems to have been first introduced into cultivation in 1793, at Kew, and came from Jamaica. The date of its American introduction I have not yet been able to discover, although this is a matter of consider-

* There is a great deal of confusion in the trade use of the names "sword fern," "Boston fern," and *Nephrolepis exaltata*. In Florida, Dr. J. K. Small tells me the wild species, *N. exaltata*, is called "Boston fern," and the term "sword fern" is applied to the other Florida species, *N. biserrata*, a very different thing. Several florists, at least, list as *N. exaltata*, the dissimilar *N. cordifolia*, a further element of confusion.

able interest, especially with respect to the origin of the variety *bostoniensis*. Between 1890 and 1895 florists discovered that there were in cultivation under the name of sword fern two distinct forms, the one as above described, the other (see PLATE 13, FIG. 2) laxer, with broader leaves, upon which the sori and sporangia were small and abortive. The second form was also more rapid in growth.

There are two versions of the origin and discovery of this second form which afterward came to be known as the "Boston fern," or "Boston sword fern." According to one version, the variety was first discovered among a lot of two hundred small plants shipped as plain sword fern by the Robert Craig Company, of Philadelphia, to F. C. Becker, of Cambridge, Massachusetts. It is certain that the latter florist was among the first to recognize the importance of the second form which he at first identified as *N. davallioides*. Under this name a considerable number of plants were sold. This identification was later challenged by G. W. Oliver, of Washington, who finally convinced Becker after a considerable exchange of opinion in the Florists' Exchange* that the fern in question was at least not *N. davallioides*, or, as it should be called, *N. biserrata*. The dispute ended according to the citations referred to by September 12, 1896. Becker stated that the plant had been submitted to a fern expert by the Nomenclature Commission of the Society of American Florists, and his advertisement was changed so that the fern was listed henceforth as *N. exaltata bostoniensis*.

The other version has recently received a convincing statement in the Florists' Exchange† by F. W. Fletcher, of Auburndale, Massachusetts. According to this version, the Boston fern, when attention was first directed to it, was in the hands of several growers, particularly about Boston. Many of these growers were of the opinion that they were the discoverers of it, but there seemed to be no way of determining its real origin. At any rate it was referred to the Nomenclature Commission of the Society of American Florists as stated above, and by them submitted first to Kew, and later to G. W. Davenport. The latter is said

* 8: 23; 57; 92; 122; 814; 858. 1896.

† 40: 1134, 1135. 20 N 1915.

to have been responsible for its identification as a variety of *N. exaltata*, and the assignment of the varietal name *bostoniensis*, because of its prevalence in the neighborhood of Boston. Supporting this statement, there is a single, small, and immature, leaf of var. *bostoniensis* preserved in the Gray Herbarium with Davenport named as collector and dated in 1896.

It may be noted that the second account does not preclude the possibility that a single florist, perhaps Becker, may have been originally responsible for the discovery of the new form. It is generally admitted that he had much to do with its exploitation and dissemination. It should be added, however, that some florists are of the opinion that the form has been in existence as long as forty years. A factor of great present uncertainty lies in the possibility of errors in identification on the part of florists. At present a number of florists are offering as *N. exaltata* a very different form, the species, *N. cordifolia* or *N. tuberosa*. Absolute nomenclatorial accuracy seems still to be beyond the abilities of botanists, even systematists, so that florists may be forgiven for occasional lapses, but the occurrence of such lapses indicates that the origin of var. *bostoniensis* may necessarily remain in the category of unsolved mysteries.

The study of tropical collections of *Nephrolepis*, both living and herbarium, may throw some light on this mystery. Another source of possible enlightenment lies in a study of the sources from which this species was introduced into cultivation. The possibilities of variation in a species so widely distributed as *N. exaltata* are too great to be overlooked. It is not impossible that the variety *bostoniensis* may have had a direct importation from the tropics.

2. *Sports from var. bostoniensis*

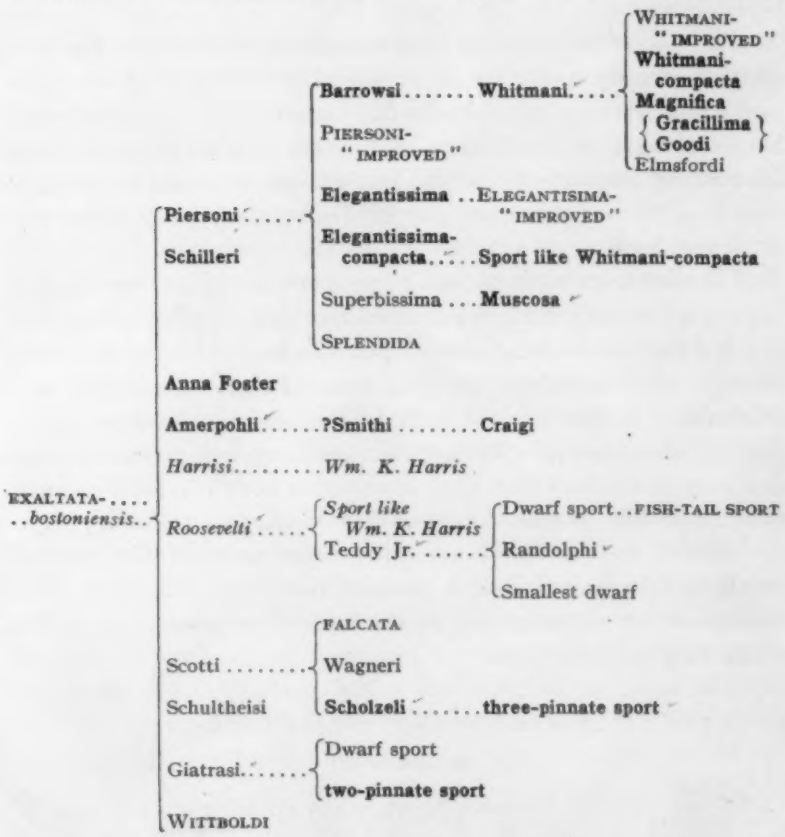
No matter what may be the uncertainty regarding the ancestry of var. *bostoniensis*, there is little or no uncertainty regarding its progeny. In the course of less than twenty years, it has given rise, directly and indirectly, to at least one hundred different forms. Its known first generation descendants probably number no more than twelve. The remaining ninety odd represent third, fourth, fifth, or even later generation sports of vegetative origin.

The forms which are claimed as direct sports from var. *bostoniensis* are as follows: *Piersoni* (PLATE 10, FIG. 2; PLATE 11, FIG. 2), *Schilleri*, *Anna Foster*, *Amerpohli* (PLATE 11, FIG. 7), *Harrisi* (PLATE 13, FIG. 3), *Roosevelti* (PLATE 13, FIG. 3), *Scotti* (PLATE 14, FIG. 2, 5), *Schultheisi*, *Giatrasi* (PLATE 15, FIG. 2) and *Wittboldi*. These forms do not represent ten diverse lines of variation, but three, or at most four or five. *Piersoni*, *Schilleri*, *Anna Foster*, and *Amerpohli* show an increase in leaf division from the once-pinnate type of var. *bostoniensis*. *Schilleri* seems to be an approximation of the form shown by *Piersoni*, which appeared more than ten years earlier. Both are twice-pinnate, as is *Anna Foster*, but the latter shows further differences in the shape and size of the ultimate segments, and other features. *Amerpohli* is thrice-pinnate, and, if directly descended from *bostoniensis*, represents a skipping of the twice-pinnate stage.

Scotti (PLATE 14, FIG. 2, 5), *Schultheisi*, and *Giatrasi* (PLATE 15, FIG. 2) are dwarf sports of var. *bostoniensis*. *Schultheisi* seems to be an approximate repetition of *Scotti*, ten years afterward. *Giatrasi* is well distinguished from the other two dwarfs in characters of growth habits, leaf form, etc., so that there may be said to be at least two distinct kinds of dwarf sports.

Harrisi and *Roosevelti* (see PLATE 13, FIG. 3) are almost exactly alike in respect to the leaf characters, but both differ from var. *bostoniensis* in having the pinnae more wavy or undulate, due to an increase in the parenchymatous part of the pinnae especially along the margin. *Wittboldi*, for which a spore origin is claimed, was originally described as "twice as wide as var. *bostoniensis*, and with wavy pinnae." As yet I have no surely authentic plants, and so cannot speak with certainty. The original introducers do not have the plant in stock now, but the material at hand named *Wittboldi* indicates that var. *bostoniensis* was probably not the parent form. The new form may have arisen as a chance sporeling, the result of the accidental introduction of some entirely different form, a very frequent occurrence in greenhouses. Herbarium specimens from Florida indicate that there may also be a "fish-tail" sport of var. *bostoniensis*, not included in the list of sports named above. There have probably been a few other variations of var. *bostoniensis*, either like those already named, or so unsatisfactory from the florists' point of view that they have not been preserved.

Eliminating the last two mentioned types, *Wittboldi* and the "fish-tail" form, there remain then three main lines of variation from var. *bostoniensis*, namely: a line showing increased division in the leaf, a line showing increased waviness or ruffling of the



GENEALOGICAL CHART OF PROGRESSIVE SPORTS OF *bostoniensis*

Black face type indicates division sports.
Italics indicate sports showing ruffling.
Plain Roman type indicates dwarfing.
Small capitals indicate other kinds of variation.

pinnae, and a line showing dwarfing. These types of variations are referred to as "lines of variation" because they represent the beginning of the orthogenetic series already mentioned, series in which these three kinds of variation are repeated in intensified

form in one or more further vegetative generations. In these three lines occur all the illustrations of progressive orthogenetic variation about which this paper is mainly concerned. Reversion or regressive variation is also common, but need not be considered here.

The variations classified as progressive according to the distinction already made are all arranged according to their origin in the chart on page 219. It should be understood that no attempt has been made at this time to include the English forms, as they are not yet available for study, but enough is known to indicate that they do not represent any kind of variation not shown by American forms.

The direct sports from var. *bostoniensis* are of further interest in connection with the present discussion only as they have given rise to progressive variations. Upon this basis we may eliminate at once the varieties, *Schilleri*, *Anna Foster*, *Schultheisi*, and *Wittboldi*. It does not follow that these varieties have no potentialities of variation. Their failure to vary has probably been due only to the fact that they have never been extensively cultivated, and this in turn, has been due to the fact that they have not offered to the florist sufficient inducement in the way of horticultural possibilities. It remains then to consider the other *bostoniensis* sports according to the lines of progressive variation which they exhibit.

3. *Progressive division of the leaf*

(PLATES 10–12)

Of the original *bostoniensis* varieties showing an increase in leaf division, *Piersoni* is of most importance. From this form have come three or possibly four types of sports, viz., varieties showing further increase in division, *Barrowsi*, *elegantissima*, and *elegantissima-compacta*: varieties showing dwarfing, *superbissima;* a variety with forked pinnae, *splendida;* and a so-called "improved" form, *Piersoni* "improved."

Piersoni represents a twice-pinnate sport from the once-pinnate var. *bostoniensis*. *Barrowsi* shows a slight increase in the lobing of the pinnulae, that is, it is twice-pinnate pinnatifid. *Elegan-*

tissima (PLATE 12, FIG. 1) and *elegantissima-compacta* (PLATE 12, FIG. 2) are, however, more divided, in some leaves as much as thrice-pinnate. *Elegantissima-compacta* is of further interest because it is also a dwarf, thus combining two lines of variation at once.

Piersoni "improved" illustrates a type of variation which is of special interest to florists, and to which they seem generally to apply the name "improved," as, for example, *elegantissima* "improved" and *Whitmani* "improved." All the forms in the division series revert more or less, that is, throw once-pinnate leaves, and sometimes runners, *i.e.* plants which revert as a whole. The florist objects to these mixed plants and selects for greater stability. When he obtains stock showing less reversion, he is likely to call it "improved." There is great variation in the matter of reversion. Some kinds are relatively stable from their first appearance, others may produce as many reverting leaves as of the new type. Usually in order to keep stock true to type, a florist must exercise care in the selection of the runners which are used as stock plants.

Another illustration of dwarfing from *Piersoni* apparently of a brachyotic nature is represented by the variety *superbissima* (PLATE 12, FIG. 4), which is much less than half as long as its parent form. The dwarfing has been achieved mainly by a radical shortening of the rachis, with proportionately less decrease in the size of the pinnae. The resulting leaf is dense, stiff and twisted, of no particular grace, but interesting as an oddity. Like *Piersoni*, *superbissima* exhibits considerable reversion, and as yet no certain "improved" or non-reverting form has been obtained.

The sixth sport of *Piersoni* which may be classed as progressive, exhibits the kinds of variation prevalent though not common throughout the fern order, that is, the forking or dichotomy of the leaf apex or of the segments. In this form, called *splendida* (PLATE 12, FIG. 3), the pinnae show the forking, and a single plant may bear at one time several kinds of leaves, once-pinnate, twice-pinnate, and forking.

Referring again to the form *superbissima*, it may be noted here that from this there has come, as from *Piersoni* itself, a further sport showing progressive increase in the division of the leaf.

This variety is called *mucosa* (PLATE 12, FIG. 6) because of the dense, finely divided condition of the leaf. It seems to represent the same amount of division of leaf as is seen in the forms *elegantissima* and *elegantissima-compacta*, that is, it is thrice-pinnate. Tracing the ancestry of *muscosa*, we find the four forms, *bostoniensis—Piersoni—superbissima—muscosa*, which are, respectively, one-pinnate, two-pinnate, dwarf, and three-pinnate.

Two generalizations are suggested by the facts shown in the preceding series, and borne out by others to be shown later, which, if thoroughly understood, will simplify the description and explanation of the remaining forms. They rest not only on these few examples, but, as will appear, are true in the case of nearly all the variations considered in this paper.

1. Progressive variation takes place naturally along the three lines already described, viz., increase in leaf division, increase in ruffling or crisping, and dwarfing.

2. Any form which has not reached the limits of possibility in variation along the first and last mentioned lines, may be expected to give rise to new forms showing further progressive variation in one or both of them.

To particularize, we may say that any once-pinnate form may be expected to give rise to a twice-pinnate variety. A twice-pinnate variety may be expected to give rise to a thrice-pinnate form. The most highly divided form which has so far appeared is five times pinnate (see PLATE 10, FIG. 5; PLATE 11, FIG. 6), and there appear to be constitutional physiological reasons why further division is unlikely. As is the case in the progressive division in the leaf, so also with dwarfing or pumilism. Any large form whether once- or twice-pinnate, may be expected to give rise to a dwarf variety, as *superbissima* was derived from *Piersoni*, and as dwarf forms have occurred in the other series to be described below. With respect to progressive increase in ruffling, it is uncertain whether the second generalization applies to this line of variation or not. It may be that it does not apply in this line at all, or it may be that in the division series, a change in the degree of waviness would be too relative to admit of exact determination. It is certain that dwarfing occurs in all three lines, and that increase in division occurs also in the dwarfing series. Whether

increase in division also occurs in the frilled or ruffled series is yet to be determined.

Of all the varieties of *Piersoni*, *Barrowsi* is perhaps of greatest interest because it has given rise to at least two further generations (vegetative) of division sports. From *Barrowsi* has come *Whitmani*, a clear increase in division, and from *Whitmani* have come several sports showing still more division.

Of the sports of *Whitmani* (PLATE 10, FIG. 3; PLATE 11, FIG. 3) named on the chart, *Whitmani* "improved" represents a more stable form, *i.e.* less given to reversion. *Whitmani-compacta* is a trifle smaller than its parent form, and has a fuller leaf with more expanded segments. *Goodi* and *Gracillima* (PLATE 11, FIG. 4; PLATE 12, FIG. 5) are apparently separate occurrences of the same variety, entirely thrice-pinnate, and with smaller segments than *Whitmani*. It may represent a dwarfing. *Magnifica* (PLATE 10, FIG. 4; PLATE 11, FIG. 5) is clearly four times pinnate, and represents the greatest amount of division which can be definitely stated to have been evolved in this particular series. *Elmsfordi* (PLATE 12, FIG. 7), a reputed spore sport, looks much like a miniature *Whitmani*, being less than half its size. It is different in another particular, in that it produces a much greater number of leaves to each crown, and in a given size pot. A plant grown to full size in a four-inch pot may show as many as a hundred leaves. In a twelve-inch pan, an estimate of a thousand leaves appeared conservative.

The other progressive sports in the *Piersoni* line are sufficiently described for the present by the typography of the chart and by the figures in plates 10–12.

The other reputed *bostoniensis* sport from which further progressive variations in the line of division are believed to have come is *Amerpohli*, a thrice-pinnate variety. *Amerpohli* in leaf division is very like *magnifica*, and in growth habit and carriage of the leaf it is also similar. Because of this close resemblance it is more than reasonable to suggest that it may really have come from *Whitmani* as a sport and that its reputed origin from var. *bostoniensis* may be an error. From *Amerpohli*, the four times pinnate form, *Smithi*, is said to have come. There is some question as to the correctness of this assertion but none regarding the fact that from

Smithi a five times pinnate form, *Craigi* (PLATE 10, FIG. 5; PLATE 11, FIG. 6), has come. This form is particularly interesting as exemplifying what is at present the highest amount of leaf division that has been attained by these forms. *Craigi* is illustrated in the plate with *Piersoni* not as necessarily derived from this but in order to complete the possible series of division forms. In that plate *Barrowsi* has been omitted because I have not yet been able to get a mature leaf of it.

As appears most noticeably on the plates illustrating these division forms, the increase in pinnation seems generally to be accompanied by a striking decrease in the size of the leaf, that is, in the total area. It is probable, however, that the actual leaf surface area remains the same, the apparent decrease being compensated for by the multiplication of the segments which may even expose more actual surface.

4. *Progressive increase in ruffling of the leaf*

(PLATE 13)

The series showing progressive increase in ruffling or crisping of the leaf begins with the original species, *N. exaltata* (PLATE 13, FIG. 1), because one of the characters in which var. *bostoniensis* (PLATE 13, FIG. 2) departs from the typical *N. exaltata* is in this feature. From var. *bostoniensis* there have been two more ruffled sports, *Harrisi* and *Roosevelti*, almost duplicating each other in appearance, but well distinguished as regards their progeny. PLATE 13, FIG. 3, may represent either *Harrisi* or *Roosevelti*, and PLATE 13, FIG. 4, may represent the variety *Wm. K. Harris*, or a coördinate form of similar appearance derived from *Roosevelti* but unnamed. Both are alike in leaf characters including crisping of pinnae, and both represent the highest development of this character which has been obtained in a direct progressive series. It will be noted that with the increase in crisping there has come also a tendency to develop auricles on the pinnae. This is of interest because it is a feature characteristic of wild varieties of other fern species.

The form described above represents the final sport so far obtained from the *Harrisi* line. From the *Roosevelti* line, how-

ever, two additional generations have appeared, showing progressive dwarfing. The first, called *Teddy Jr.* (PLATE 13, FIG. 5), has the characteristics appropriate to the principles of its namesake, as it appears to be the most prolific in producing new progressive variations of any *Nephrolepis* form. These new variations have appeared in three forms, but the interesting feature about them is that they are apparently common wherever *Teddy Jr.* is grown. In other words, *Teddy Jr.* shows a high frequency of variation.

Teddy Jr. is about half the size of the parent form *Roosevelti*. The three new forms are further dwarfs as shown in PLATE 13, FIGS. 6–8, respectively, the last being the smallest of the three and perhaps brachyotic. Only one, the middle-sized one, has been named as yet, being called *Randolphi* (FIG. 7) or "Baby Randolph." The smallest form may come directly from *Teddy Jr.* or it may also, according to report, arise as a sport from the largest of the three *Teddy Jr.* dwarfs.

It will be noted that the illustrations indicate that the amount of frilling continues to increase in the successively smaller forms. This increase, however, is probably to be correlated with the dwarfing, and should not be interpreted as in the line of progressive increase in ruffling.

From the largest of the three dwarf sports from *Teddy Jr.* there has just come to my attention a fish-tail sport, a form of variation apparently possible in all ferns.

5. *Progressive dwarfing*

(PLATES 14 AND 15)

Finally we have the series showing progressive dwarfing directly from var. *bostoniensis*. This seems to have occurred in three separate instances. The forms *Scotti* (PLATE 14, FIGS. 2, 5) and *Schultheisi* appear to be very similar, but independently derived. Of these *Scotti* is particularly interesting because it has given rise to other sports. *Giatrasi* (PLATE 15, FIG. 2) is also interesting for the same reason, and because it has distinctive features of its own. Neither of these dwarfs seems to be brachyotic.

Scotti (PLATE 14, FIGS. 2, 5) differs from var. *bostoniensis* not only

in being smaller, but also in having blunter more wavy pinnae, and in having both leaves and pinnae more or less arched. From *Scotti* have come dwarf and division sports, as well as a fish-tail form. The further dwarf is called *Wagneri* (PLATE 14, FIGS. 3, 6), and seems to represent merely a foreshortening of the *Scotti* form with an intensification of the arching.

The division sport of *Scotti* is called *Scholzeli* (PLATE 14, FIG. 7), and is practically a miniature *Piersoni* in the type of division, shape of pinnae, et al. From *Scholzeli*, a two-pinnate form, has come a three-pinnate sport (PLATE 14, FIG. 8) to which no separate name has been given. It has been sold as *Scholzeli*. It corresponds to *Whitmani* in the division series proper, and like this would undoubtedly give rise to a four-pinnate form if grown in sufficient numbers.

Giatrasi (PLATE 15, FIG. 2) is little more than half as large as *Scotti*, and differs further in being slower growing, in producing a larger number of leaves per crown, and in the characteristics of individual leaves as well. These are thinner, have undulating rachides, and the pinnae are shorter and blunter. Because of its slower habits of growth, it appears to have found favor only with its introducer, George Giatras, in whose establishment some five to ten thousand plants are grown each year. Under these conditions it has given rise to two further sports, both as yet unnamed. One of these is a further dwarf (PLATE 15, FIG. 3), and the other is twice-pinnate (PLATE 15, FIG. 4). These new forms seem to partake of the slower growth habits of *Giatrasi*, and are therefore unlikely ever to be grown in quantity. This is unfortunate from a scientific point of view, as their further development and possible sports would be of considerable interest.

C. GENERAL CONSIDERATIONS

Some general considerations suggest themselves as a result of the foregoing descriptions; for example, the character and significance of the reversions, the possibilities of spore reproduction and segregation of forms, the possible results of morphological and cytological studies, etc. Nothing, however, is to be gained by speculation along these lines in the absence of additional facts. The reversions are under observation, and I hope that another

growing season may allow the accumulation of sufficient information to make possible a description of these forms. Furthermore, the forms which have been so incompletely described in the preceding pages are worthy of a more careful and detailed study and description. I hope also to start spore cultures within a few weeks, using not only material known to be spore-fertile, but also forms presumably spore-sterile in the hope that apospory may result. There are indications that this phenomenon may occur.

Before concluding the present consideration, there are, however, two or three phases of the topic to which attention should be directed, by way of emphasis upon the significance of the variations which have been described.

First, further emphasis should be laid upon the separateness of the forms inter se. They are entirely discrete and distinct, and in this respect, are in accord with the characteristics ascribed to mutations. The individuals of a given variety show great uniformity under any given conditions of cultivations, and do not pass by imperceptible differences into related varieties. The fact that reversion takes place does not alter the separateness of the different varieties. In fact the reversions themselves furnish the best possible evidence of the distinctiveness and lack of continuity between even closely related varieties. The truth of this statement is established by the fact that the reversions are rarely if ever complete. A twice-pinnate variety may show some once-pinnate leaves and may give rise to new plants with once-pinnate leaves, but these once-pinnate leaves do not show a complete return to the form, size, etc., of the leaves of the original once-pinnate variety. The leaves of the reverted plant tend always to retain something of the character of the twice-pinnate plant. It appears then that the process by which the twice-pinnate form was produced from the original once-pinnate form must represent a protoplasmic change which is retained to some extent, even in the reversion. I cannot say that reversion may never be complete, but I have not yet found any cases where it is. This fact, however, that in any given progressive variation, a constitutional change is effected so pronounced that it can rarely if ever be completely reversed, is striking evidence that the varieties formed by progressive variation are distinct and discontinuous.

One of the interesting morphological possibilities is found in a problem under study, to determine whether new bud sports do not always appear first in the form of a variant leaf on the parent plant, this leaf showing the line of variation which the new form afterward fulfills. The solution of this problem depends on the possibility of determining whether each leaf has a subtending runner, and whether all the new plants from a given runner are alike and partake of the characteristics of the connected leaf. The problem, stated in other words, is to determine whether the actual process of variation takes place first in the cells of the leaf and is repeated in the runner and its sports, or whether the variation may not take place in the runner itself.

The fact that varieties in the division series do not always differ *inter se* merely by division, but also sometimes in the size and shape of the segments et al., and the further fact that other variations occur, such as dwarfing and ruffling, are in opposition to the conclusions reached by R. G. Leavitt,* who suggested that the appearance of varieties showing an increase in division was due merely to a translocation of the ability to divide from the whole leaf to the pinnae, a phenomenon to which he applied Bateson's term of homoeosis. To accept the hypothesis of such a translocation, it would be necessary to find that the twice-pinnate form differs from the once-pinnate form, from which it arose, merely in the amount of division, a supposition which is hardly supported by facts.

A further argument for the hypothesis of homoeosis adduced by Leavitt, and applied not only to these ferns but also, for example, to the horse-chestnut, lay in the fact that the new forms possessed no utilitarian advantage over their parents. The fact that the horse-chestnut leaf cuts off each pinna by a distinct callus as well as its petiole base, and that this double *decision* appears to have no adaptive value, was advanced as confirmatory of the homoeosis thesis. This is interesting, but will hardly be accepted as an argument in view of modern objections to teleological explanations. It may be noted that Eimer, twenty and more years ago, made a most determined stand against the belief that adaptability was a prime necessity in the appearance of new characters and the evolution of new forms.

* Bot. Gaz. **47**: 30–68. Ja 1909.

With respect to the present group of horticulturally produced forms, it appears evident that the lack of adaptability to natural conditions shown by most of them would prevent their establishment if they were to be introduced. This statement is probably true for the original sports of var. *bostoniensis* as well as for the forms of later vegetative generations, and this fact in itself is an adequate explanation of the non-occurrence of any of these forms wild. On this assumption they represent new forms produced in the course of evolution, most of which would be eliminated by the discriminating agency of natural selection. They differ therefore from wild forms showing the same types of variation, only in their non-adaptability. Certainly the three lines of variation along which these forms of *Nephrolepis* have been differentiated, and especially the lines of increase in division and dwarfing, can be paralleled by similar lines of variation among wild forms which have succeeded better because provided with the means to meet natural conditions of competition, etc. Certainly also the forms described in this paper comprise, within their extremes of variation, greater differences than are required for the differentiation for many natural species. For example, differentiation of species and even genera on the basis of leaf division is too common, not only among ferns but also among flowering plants, to require more than mention.

As possible corollaries to the statements of the preceding paragraphs, two points are of interest and may be indicated in the form of questions. Is the rapidity of evolution of these *Nephrolepis* varieties, fifty or more in fifteen years, any indication of the speed of evolution of wild forms of similar distinctiveness? Or does the fact, that nearly all if not all of these forms would lose out in the struggle for existence, indicate that, while the appearance of ill-adapted variations may be common, the appearance of successful variations is most uncommon?

In the preceding paragraphs it has been assumed that the variations of these cultivated ferns are homologous with similar variations occurring among wild species. If this is true, (that the two lines of variations are homologous) it is not improbable that the causes may be similar. These causes may be sought by experimental methods, by the cultivation of a variety which shows a

relatively high coefficient of variability, as for example, *Teddy Jr.* They may be sought by cytological study of similar variations, as is shown by the production of dwarfs in many widely separated lines, or by the reversions. The cytological method would only show some possibly correlated facts of cell structure. The experimental method might show some connection between cultural methods and the appearance of new forms. In this connection it may be noted that Eimer and Coulter, perhaps the earliest and the latest to discuss the possible causes of orthogenetic variation, have both professed the opinion that climate is the probable causative agency.

The query has been expressed as to whether a hybrid origin might not account for these variations of *bostoniensis*. With this possibility in mind, one species of *Nephrolepis*, *N. biserrata*, which is co-extensive with *N. exaltata* in distribution, would seem to be worthy of investigation. It is hard to imagine, however, how the combination of any two twice-pinnate species of *Nephrolepis*, or indeed of any more dissimilar species, could account for the appearance not only of the three lines of variation but of the progressive intensification of these lines thereafter. The sterility of these forms is apparently the only feature these forms have in common with most hybrids, and this must presumably be accounted for in some other way.

For the present, all that can be said as to the genesis of these forms is they apparently proceed from some internal cause. It may be added that similar variations have occurred as a result of spore sporting, and also that similar variations are common wild. These forms may therefore be considered as indicating how species, showing similar differences, have arisen, that is, by what lines of variation. The evidence offered along this line by the progressive forms alone is most incomplete, however, without an understanding of the regressive variations as well.

D. SUMMARY OF FACTS AND CONCLUSIONS

1. *Nephrolepis*, a genus of once-pinnate tropical ferns, includes several species which are cultivated. Nearly all of these cultivated species show variation by bud sports, but *N. exaltata* through its variety *bostoniensis* is most prolific, having given rise

to more than one hundred different forms in less than fifteen years.

2. Cultural conditions are such as to favor the appearance and preservation of variations, because the soil and other environmental conditions are probably practically perfect, and because very large numbers of plants, one to two million, are grown per annum in the United States alone.

3. The variations may be classified under two headings, progressive, and regressive or reversive. Progressive varieties are defined as those which show less resemblance to var. *bostoniensis* than their parent forms. Regressive varieties are defined as those which show something of a return in characters toward var. *bostoniensis*.

4. Progressive variations have appeared along three main lines, viz., those showing increased division of the leaf; those showing increased ruffling of the pinnae; those showing dwarfing. Variations showing dichotomy of the pinnae and leaf tips also occur.

5. Progressive increase in division has gone through five vegetative generations, each succeeding step being an intensification of the preceding, the forms varying from once to five times pinnate. Progressive increase in ruffling has gone through three vegetative generations. Progressive dwarfing has gone through three vegetative generations.

6. The dwarfing seems to be clearly of two sorts: first, brachyotic or unilinear; and second, normal in all dimensions. More than one type of division sport is also indicated.

7. Progressive increase in leaf division and progressive dwarfing may be expected in any form which has not reached the limits of variation along these lines.

8. Regressive variations rarely if ever show complete return to their parent forms or to var. *bostoniensis*.

9. The indicated coefficient of variation for progressive variations is very low; probably between one in one million and one in one thousand. Regressive variation is much more common.

10. The variations are all discrete or discontinuous, not proceeding by imperceptible differences.

11. The progressive variations in their differences actually

parallel the differences existing between many wild species of ferns and flowering plants.

12. The main difference between these variations and those shown by wild forms lies in the fact that these horticultural forms do not possess adaptability to natural conditions. In most cases, with the variation, has come decreased vigor of growth.

13. The cause or causes of these variations are undetermined. They proceed as if from internal stimulation. The improved cultural conditions do not appear as causes, but rather as a means of preserving forms which, under wild conditions, would be eliminated by natural selection.

E. INDEX OF THE SPORTS DESCRIBED ABOVE

VARIETIES SHOWING INCREASE IN LEAF DIVISION

Name	Producer
Anna Foster	Lucias Foster, Dorchester, Mass.
Barrowsi	Henry Barrows, Whitman, Mass.
Amerpohli	Edward Amerpohl, Janesville, Wis.
Elegantissima	F. R. Pierson, Tarrytown, N. Y.
Elegantissima-compacta	F. R. Pierson, Tarrytown, N. Y.
Elegantissima "improved"	F. R. Pierson, Tarrytown, N. Y.
Giatrasi	George Giatras, West Hoboken, N. J.
Goodi	Good & Reese, Springfield, Ohio.
Gracillima	Henry Barrows, Whitman, Mass.
Craigi	Robert Craig, Philadelphia, Penn.
Magnifica	Henry Barrows, Whitman, Mass.
Muscosa	F. R. Pierson, Tarrytown, N. Y.
Piersoni	F. R. Pierson, Tarrytown, N. Y.
Schilleri	J. L. Schiller, Toledo, Ohio.
Scholzeli	Herman Scholzel, New Durham, N. J.
Scholzeli, three-pinnate sport	Herman Scholzel, New Durham, N. J.
Smithi	John Clark, Washington Botanic Garden, Washington, D. C.
Whitmani	Henry Barrows, Whitman, Mass.
Whitmani compacta	Henry Barrows, Whitman, Mass.
Whitmani "improved"	Henry Barrows, Whitman, Mass.
Elegantissima sport, like Whitmani compacta	George Giatras, West Hoboken, N. J.

VARIETIES SHOWING PROGRESSIVE RUFFLING

Name	Producer
Var. bostoniensis	?F. C. Becker, Cambridge, Mass.
Harrisi	Wm. K. Harris, Philadelphia, Pa.
Wm. K. Harris	Wm. K. Harris, Philadelphia, Pa.

Roosevelti	American Rose & Plant Co., Springfield, Ohio.
Roosevelti sport, like Wm. K. Harris.	American Rose & Plant Co., Springfield, Ohio.

VARIETIES SHOWING PROGRESSIVE DWARFING

Name	Producer
Elegantissima-compacta	F. R. Pierson, Tarrytown, N. Y.
Elmsfordi	Scott Bros., Elmsford, N. Y.
Giatrasi	George Giatras, West Hoboken, N. J.
Giatrasi, dwarf sport of	George Giatras, West Hoboken, N. J.
Schultheisi	Anton Schultheis, College Point, N. Y.
Scotti	John Scott, Brooklyn, N. Y.
Superbissima	F. R. Pierson, Tarrytown, N. Y.
Wagneri	Peter Wagner, Brooklyn, N. Y.

VARIETIES SHOWING DICHOTOMY OF PINNAE

Name	Producer
Falcata	Peter Wagner, Brooklyn, N. Y.
Splendida	Good & Reese, Springfield, Ohio.

VARIETY OF UNCERTAIN CHARACTER

Name	Producer
Wittboldi	Wittbold, Chicago, Ill.

Explanation of plates 10–15

All photographs made to about the same scale except on Plates 11 and 14.

PLATE 10

Leaves illustrating a division series. FIG. 1. Var. *bostoniensis*. FIG. 2. *Piersoni*. FIG. 3. *Whitmani*. FIG. 4. *Magnifica*. FIG. 5. *Craigi*.

PLATE 11

Pinnae illustrating a division series. FIG. 1. Var. *bostoniensis*. FIG. 2. *Piersoni*. FIG. 3. *Whitmani*. FIG. 4. *Goodi* (or *gracillima*). FIG. 5. *Magnifica*. FIG. 6. *Craigi*. FIG. 7. *Amerpohli*.

PLATE 12

Illustrating one secondary and four direct sports of *Piersoni*. FIG. 1. *Elegantissima*. FIG. 2. *Elegantissima-compacta*. FIG. 3. *Splendida*. FIG. 4. *Superbissima* (small leaf). FIG. 5. *Goodi* (or *gracillima*). FIG. 6. *Muscosa*. FIG. 7. *Elmsfordi*.

PLATE 13

Illustrating variations in ruffling and dwarfing. FIG. 1. *Nephrolepis exaltata*. FIG. 2. Var. *bostoniensis*. FIG. 3. *Harrisi* (or *Roosevelti*). FIG. 4. *Wm. K. Harris* (or new sport of *Roosevelti*). FIG. 5. *Teddy Jr.* FIGS. 6–8. Dwarf sports of *Teddy Jr.* FIG. 7. *Randolphi*.

PLATE 14

Pinnae illustrating dwarfing and sports of *Scotti*. FIG. 1. Var. *bostoniensis*. FIG. 2. *Scotti*. FIG. 3. *Wagneri*. FIG. 4. *Falcata*. FIG. 5. *Scotti*. FIG. 6. *Wagneri*. FIG. 7. *Scholzeli*. FIG. 8. Three-pinnate sport of *Scholzeli*.

PLATE 15

Illustrating dwarfing and sports of *Giatrasi*. FIG. 1. Var. *bostoniensis*. FIG. 2. *Giatrasi*. FIG. 3. Dwarf sport of *Giatrasi*. FIG. 4. Two-pinnate sport of *Giatrasi*.

The vegetation of Connecticut
V. Plant societies along rivers and streams*

GEORGE E. NICHOLS

(WITH ELEVEN TEXT FIGURES)

In the present series of papers on the vegetation of Connecticut, the principle of succession has been adopted as the most satisfactory basis for classifying plant associations. This scheme of classification, it may here again be remarked, treats vegetation both from a genetic and a dynamic standpoint. It recognizes the fact that plant societies, or associations, as they exist today, are the product not alone of contemporaneous conditions, but of past conditions as well. It also emphasizes the fact that the plant associations of today are not necessarily permanent, but are liable to change through the influence of various factors.

In the third and fourth papers of the series,† attention was directed to the plant associations of uplands and of lowlands. There the changes in vegetation, and therefore the succession of plant associations, are influenced primarily by plant and animal agencies—in other words, by biotic factors. There remain to be considered, then, successions which are associated not only with biotic factors but with topographic factors as well. Succession of this sort has been termed TOPOGRAPHIC SUCCESSION. Topographic succession is seen principally along rivers and streams and along the coast. The present paper deals with plant societies along rivers and streams. Some of these societies might almost equally well have been treated along with the societies of uplands and of lowlands; yet, on the whole, so marked may be the impress of a stream on the vegetation at its margin, and so closely linked may be the development of the one with that of the other that the two cannot well be treated separately.

* Contribution from the Osborn Botanical Laboratory.

† Torreya 14: 167–194. 1914; Bull. Torrey Club 42: 169–217. 1915.

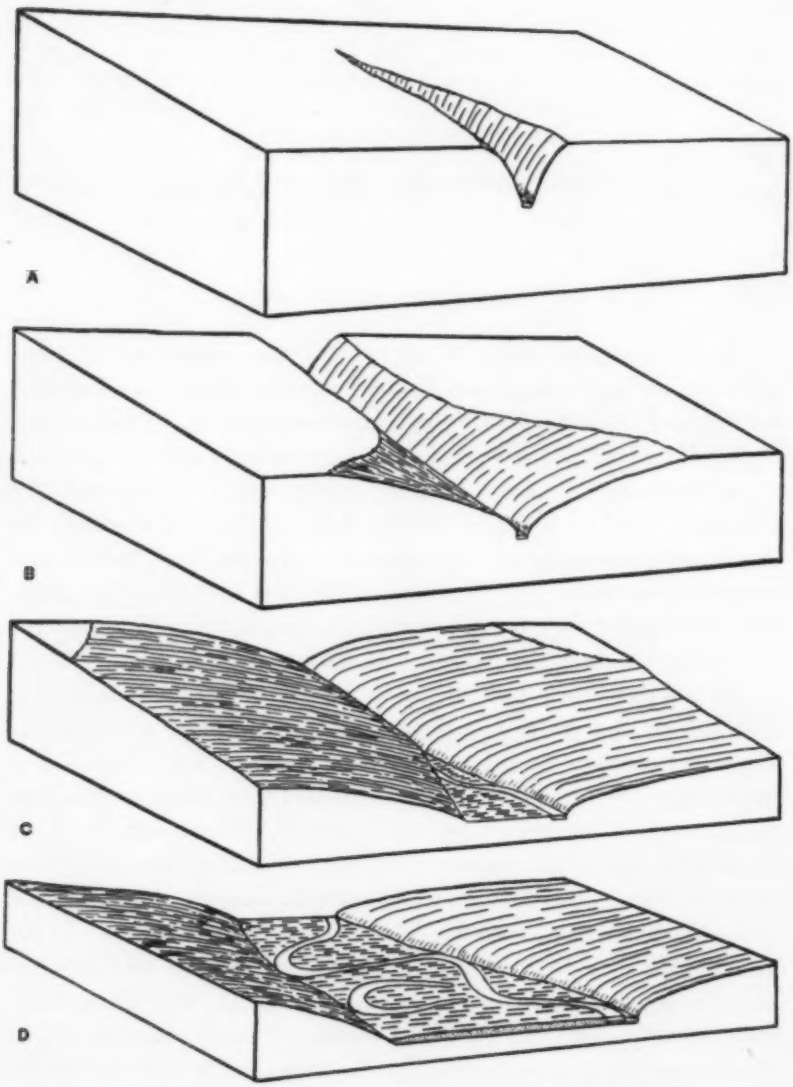


FIG. 1. Diagrams showing various stages in the development of a river.

THE LIFE HISTORY OF A RIVER

Various stages in the life history of a river are graphically represented in FIG. 1. In a young stream the current is swift and wears away the floor and sides of its channel. Vertical erosion,

however, is greater than lateral, so that the stream may gradually intrench itself in a narrow ravine or canyon. At this stage of stream development vegetation is largely confined to the flanks of the ravine. During the course of time, as the channel is cut deeper and deeper, downward erosion proceeds more and more slowly, ultimately ceasing altogether, while lateral erosion becomes correspondingly more pronounced; so that, as the stream approaches maturity, it comes to occupy a broad valley which it has carved out for itself. Vegetation covers both the bordering bluffs and the floor of the valley. As the level of the stream approaches the level of the water at its mouth, the current becomes sluggish and aggradation largely succeeds degradation. An old age river meanders about in broad, sweeping curves on the flood plain which it has built up out of sediment derived from younger parts of its system. A very distinctive type of vegetation is developed on flood plains.

Of course, the rate at which the topographic changes outlined in the preceding paragraph are effected varies widely according to the nature of the rock formations concerned. The scouring out of a ravine in clay or gravel, for example, may proceed with comparative rapidity, but the erosion of a ravine in rock is extremely slow. Ravines in glacial till and outwash have been developed since the retreat of the glaciers, and may even now be observed in the process of active formation. In most rock ravines, on the other hand, the topographic changes since the ice age have been practically negligible. The bearing of these facts on the nature of the vegetation will be referred to in later paragraphs (pp. 245, 249).

ROCK RAVINES

Occurrence and General Features.—Throughout the region under discussion the rock ravine is the common type. It abounds in the highland districts, and in the Central Lowland is frequent along the trap ranges and elsewhere. Owing mainly to the nature of the rocks concerned, canyons with overhanging or perpendicular walls are absent. The predominant type of rock ravine (FIG. 2) is somewhat V-shaped in cross section, often narrow and precipitous below but broadening out above. Toward the bottom the vegetation may be restricted to such forms as can cling to the

rock face or maintain a foothold in crevices, but higher up the sides are usually forested.

There are, of course, all sorts and sizes of ravines. In the remarks on the nature of ravine vegetation which follow, the

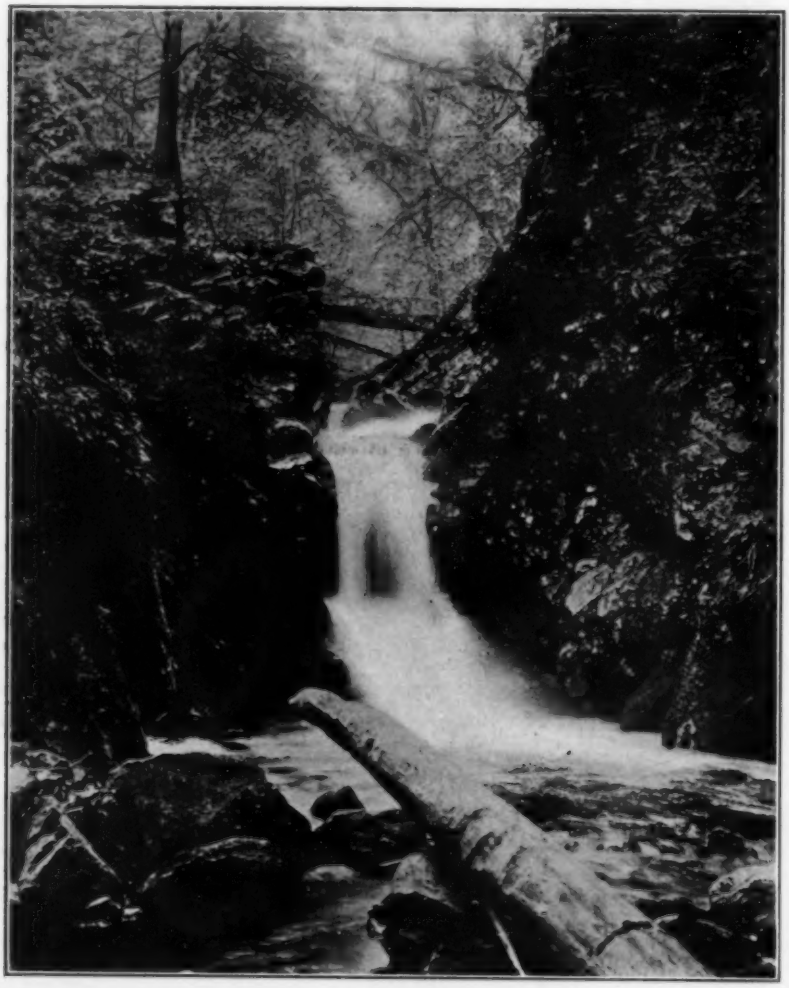


FIG. 2. Precipitous rocky slopes along stream in Sage's Ravine, Salisbury. The cliffs in the foreground are covered with mosses and liverworts.

writer has in mind a number of unusually good examples, such as Sage's Ravine and the Wolf Den in Salisbury, the Glen along Spruce Brook at Beacon Falls, Wintergreen Falls ravine in

Hamden, Woodbridge Glen in Woodbridge, Roaring Brook ravine in Cheshire, Devil's Gulch in Branford, and Ninevah Falls ravine in Killingworth. Most of these are ravines of considerable depth and have a good-sized brook at the bottom. To shallower, less well-developed ravines the remarks naturally may not be equally applicable.

The Bryophytic Flora of Rock Ravines.—Perhaps the most striking feature of the vegetation near the bottom of a ravine (FIG. 2) is the rich display of mosses and liverworts. In the stream itself, attached to rocks but always submerged, grow various aquatic forms, such as *Fontinalis*. Other more or less hydrophytic species cover the low-lying, wet and frequently submerged rocks along the margin and in the bed of the stream, mantle the spray-dashed rocks at the foot of waterfalls, and form extensive mats even in rapids and similar precarious situations. The following more or less hydrophytic species may be looked for in such places:

Chiloscyphus rivularis	*Oxyrrhynchium rusciforme*
Scapania undulata	*Amblystegium fluviatile*
Porella pinnata	*Amblystegium irriguum*
Fontinalis dalecarlica	*Hygrohypnum dilatatum*
Fontinalis gigantea	*Hygrohypnum eugyrium*
Fontinalis Lescurii	*Hygrohypnum ochraceum*

Growing on periodically inundated rock surfaces, either in the bed of the stream or along its sides, are such forms as *Fissidens incurvus*, *Grimmia apocarpa*, *Racomitrium aciculare*, and *Brachythecium plumosum*. Along with these, but usually on springy banks or on continuously moist rock surfaces, where they may or may not be submerged during flood time, may occur:

Conocephalum conicum	*Mnium hornum*
Pellia epiphylla	*Mnium punctatum*
Plagiochila asplenioides	*Philonotis fontana*
Lophocolea bidentata	*Thuidium delicatulum*
Jubula pennsylvanica	*Brachythecium rivulare*
Anthoceros laevis	*Climacium americanum*
Fissidens adiantoides	*Catharinaea undulata*

Higher up on the slopes, numerous species thrive in the crevices or plaster the faces of overhanging cliffs and precipitous rocks. The following are fairly characteristic of wet or moist cliffs:

Marsupella emarginata	*Didymodon rubellus*
Plagiochila asplenioides	*Anoectangium Mougeotii*
Scapania nemorosa	*Plagiopus Oederi*
Radula complanata	*Plagiothecium denticulatum*
Lejeunea cavifolia	*Hylocomium brevirostre*
Hymenostylium curvirostre	*Thamnium alleghaniense*

Inhabiting the drier cliffs, either in crevices or on the rock face, are such forms as:

Metzgeria conjugata	*Ulota americana*
Cephaloziella Hampeana	*Bartramia pomiformis*
Porella platyphylloidea	*Hedwigia albicans*
Leucolejeunea clypeata	*Neckera pennata*
Frullania Asagrayana	*Haplohymenium triste*
Rhabdoweisia denticulata	*Anomodon attenuatus*
Grimmia conferta	*Anomodon rostratus*

The Influence of the Chemical Nature of Rocks on the Distribution of Bryophytes.—In earlier papers of this series* brief reference has been made to the influence of the chemical composition of the substratum on vegetation. In glaciated regions like Connecticut, where most soils are transported and residual soils are rare, this influence is nowhere seen to better advantage than in ravines and similar localities where there are exposures of bare rock. In Connecticut, the problem as to the effect of the chemical nature of the substratum on vegetation concerns chiefly calcareous versus potassic rocks. The granites, gneisses, schists and sandstones, which comprise the bed rock over much of this state, are for the most part rich in potassium, which is one of the principal constituents of orthoclase feldspar and of mica (muscovite and biotite). Calcium also, as one of the components of plagioclase feldspar, hornblende, and certain other minerals, is present in some of these rocks, and in the sedimentary formations—the sandstones and shales—small amounts of calcium carbonate may be included in the cementing material. But, except locally, the amount of lime in these rocks, in so far as it affects vegetation, appears relatively insignificant. The important lime-bearing formations of Connecticut are trap and marble. The former contains potassium in small amount, one or two per cent.; the latter con-

* See Torreya 13: 109, 110. 1913; 14: 185. 1914.

tains none. Trap outcrops (diabase and basalt) occur chiefly in the Central Lowland. The marble (sometimes referred to as a limestone or dolomite) forms extensive deposits in the western part of the state, particularly in the upper Housatonic Valley.

Owing to their frequently intimate association with rock surfaces, no group of plants, with the possible exception of the lichens, is better qualified to demonstrate the influence of the chemical composition of the substratum on vegetation than the bryophytes. To be sure, many mosses and liverworts apparently flourish indiscriminately on any sort of rock substratum, provided only that requisite conditions of moisture and shade are present. But a large number of species undoubtedly "prefer" either calcareous or potassic rocks, and some are confined to such substrata. A list is given below of local species which favor calcareous rocks. Nearly all of these are commonest in the marble areas of western Connecticut, and several of them have been collected only there. Some, however, occur also along the trap ranges, while a few are known from other scattered localities.

Grimaldia fragrans
Preissia quadrata
Pellia Fabroniana
Lophozia badensis
Lophocolea minor
Cololejeunea Biddlecomiae
Frullania riparia
Saelania glaucescens
Fissidens cristatus
Cratoneuron filicinum
Hymenostylium curvirostre
Tortella tortuosa
Encalypta contorta
Mnium orthorrhynchum
Plagiopus Oederi
Myurella julacea
Amblystegiella confervoides
Amblystegium noterophilum

The species cited in the next list are reputedly calciphobous (i.e. "lime-avoiding"), and are for the most part restricted to potassic rocks.

Marsupella emarginata
Sphenolobus exsectus
Scapania nemorosa
Scapania undulata
Radula obconica
Andreaea petrophila
Andreaea Rothii
Rhabdoweisia denticulata
Dicranum fulvum
Glyphomitrium incurvum
Racomitrium aciculare
Ulota americana
Pterigynandrum filiforme
Brachythecium plumosum
Sematophyllum carolinianum
Hygrohypnum dilatatum
Hygrohypnum eugyrium

The Mesophytism of the Flora in Rock Ravines.—A rock ravine, more than any other sort of habitat, affords environmental conditions congenial to pronounced mesophytic plants. Seepage water is usually abundant along the sides, there is protection from sun and wind, and the humidity of the air, as compared with the surrounding upland, is high. Certain mosses and liverworts are practically confined to such habitats. In a more arid region than Connecticut the same observation might be made with regard to many of the higher plants, but while it is a familiar fact that in this region as elsewhere the flora of rock ravines includes many of the most extreme shade- and moisture-loving ferns and flowering plants, most of the species present are equally representative of other habitats. Species intolerant of shade are largely excluded. The majority of the forms cited in earlier papers as typical of the climax forest of this region are to be found here, and not a few of the common plants of rock ravines thrive elsewhere in wooded swamps. The following list includes a number of ferns and herbaceous flowering plants which may be considered characteristic of rock ravines, though by no means peculiar to them.

Polypodium vulgare
Phegopteris polypodioides
Asplenium Trichomanes
Asplenium acrostichoides
Aspidium spinulosum
Cystopteris bulbifera
Cystopteris fragilis
Lycopodium lucidulum
Arisaema triphyllum
Smilacina racemosa
Streptopus roseus
Trillium erectum
Laportea canadensis
Pilea pumila
Solidago latifolia
Asarum canadense
Actaea rubra
Caulophyllum thalictroides
Chrysosplenium americanum
Impatiens pallida
Viola cucullata
Viola blanda
Viola rotundifolia
Circaea alpina
Aralia racemosa
Sanicula gregaria
Hydrocotyle americana
Cryptotaenia canadensis
Collinsonia canadensis

The Ravine Forest.—The intense mesophytism of a rock ravine is further accentuated by the nature of the ravine forest (FIG. 3). As a rule the hemlock and yellow birch are prominent, and more often than not they predominate. Along with them commonly

occur the sugar maple and others of the trees elsewhere cited as characteristic of the climax forest in this region. The woody undergrowth usually includes *Hamamelis virginiana*, *Kalmia latifolia*, and *Viburnum acerifolium*, while forms such as *Carpinus*

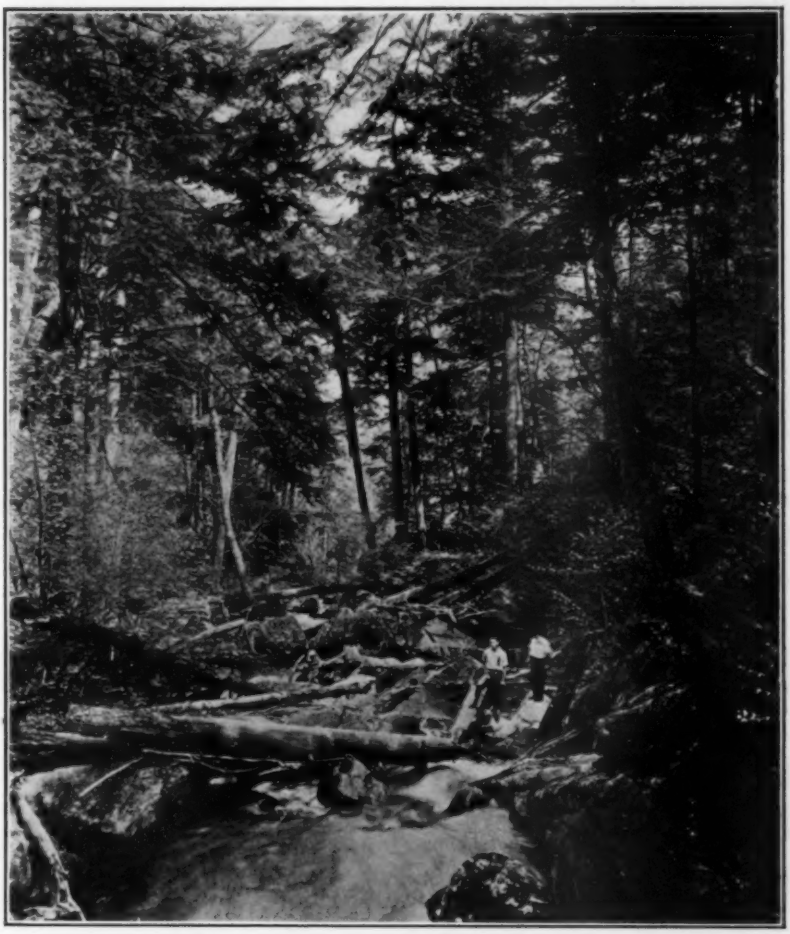


FIG. 3. Primeval forest in Sage's Ravine. Hemlock and yellow birch the common trees.

caroliniana, *Alnus rugosa* and *Benzoin aestivale*, which one ordinarily associates with swamps, frequently grow along the stream at the bottom. On the whole, ravine forests almost invariably are more mesophytic, and approximate more closely the climax

formation of this region than do the forests on the adjoining uplands. In a large measure this fact of course is due to the exceptionally favorable conditions of environment under which they have been developed. But there are other contributory causes which, while they have nothing to do with the development of these forests, may at least be partly responsible for their perpetuation. Thus, on account of their comparative topographic isolation, ravine forests may be largely immune from the fires which frequently devastate the surrounding uplands, while by reason of the difficulty in removing the timber they offer little temptation to the lumberman.

The Boreal Aspect of the Vegetation in Rock Ravines.—A few locally rare Canadian plants, such as *Lophozia alpestris*, *Lophozia attenuata*, *Gymnostomum rupestre*, *Polytrichum alpinum*, *Lycopodium Selago*, *Streptopus amplexifolius*, and *Viola Selkirkii* have been collected only in rock ravines. From an ecological standpoint, however, it is the mass-effect of the vegetation rather than the occurrence of isolated species which is significant. Many of the bryophytes, which have already been referred to as being largely restricted to rock ravines in Connecticut, are much more generally distributed farther north. But even if these rock-face and crevice forms are ignored, the stamp of the north on the vegetation here is unmistakable. The predominant trees of ravine forests are usually species of northward range. The bryophytic flora of these forests—the mossy carpet of *Bazzania trilobata*, *Hylocomium splendens*, *Ptilium Crista-castrensis* and *Hypnum Schreberi* which frequently covers the forest floor—likewise is strongly suggestive of the north. In Sage's Ravine, and doubtless elsewhere, masses of *Sphagnum* grow high up on the slopes—a common phenomenon in the Maritime Provinces of eastern Canada. Moreover, in Connecticut, many vascular plants characteristic of the north woods, while by no means confined to this sort of habitat, attain their optimum development in rock ravines. As representative of this latter group of species may be cited:

Phegopteris polypodioides	*Acer pennsylvanicum*
Taxus canadensis	*Acer spicatum*
Streptopus roseus	*Viola rotundifolia*
Actaea rubra	*Lonicera canadensis*
Oxalis acetosella	*Aster acuminatus*

On the whole, the display of Canadian plants in rock ravines is noticeably richer than in any other sort of habitat, with the exception of bogs. Various explanations for this fact may be suggested. In the first place, the atmospheric conditions here are congenial to northern plants. As compared with less protected habitats, the air is more humid, while, especially in summer, the temperature is uniformly lower and less subject to extremes. Moreover, the length of the growing season is presumably shorter than in more open situations. In a Connecticut rock ravine there may thus be reproduced in miniature a type of climate similar to that which in the Canadian Zone prevails over vast areas. In the second place, geological factors are of undoubted significance. As has already been remarked, most rock ravines have remained practically unaltered since glacial times; they represent very ancient plant habitats. It seems probable, therefore, that boreal plants which today are confined to rock ravines may formerly have been much more widely distributed, and that they have been able to persist in their present habitats because of the unusually favorable environmental conditions there afforded. In the same way it is conceivable that the present boreal aspect of the vegetation in rock ravines may be reminiscent of a one-time much more universal aspect of vegetation in this region.

RAVINES IN UNCONSOLIDATED ROCKS

The unconsolidated stony materials which form so considerable a portion of the superficial crust of the earth are not commonly designated as rocks. "Yet no line of separation can be drawn between such solid rocks as those into which the sands and muds of distant geological ages have been transformed and the semi-consolidated deposits of more recent times, or the sediments now accumulating."* In the present paper, the term UNCONSOLIDATED ROCK embraces any uncompacted rock formation, such as sand, gravel, and clay. For the sake of convenience, the word ROCK itself, written without a qualifying adjective, is used in its popular sense to include only consolidated rock formations.

Distribution, Character, and Vegetation of Ravines in Unconsolidated Rocks.—In Connecticut, ravines of this description are by

* Barrell, J. & Loughlin, G. F., Conn. State Geol. and Nat. History Survey, Bull. 13: 17. 1910.

no means uncommon. They are developed along streams throughout the Central Lowland, while in the Highlands they may occur wherever there are deposits of glacial drift. More often than not they are relatively small and correspondingly unimpressive; but in some cases, particularly in the northern half of the Central Lowland, they may assume considerable size and importance.

One of the best examples which the writer has examined of a ravine in unconsolidated rock is located in the town of Windsor. It has been scoured out to a depth of perhaps thirty feet from a coarse, sandy substratum through the activity of a small brook which flows into the Farmington River from the north. The slopes of the ravine, forested with hemlock, yellow birch, sugar maple, beech, white ash and tulip, contrast sharply with the surrounding upland which is largely overgrown with white pine, oaks, and chestnut. The undergrowth includes many of the herbaceous and shrubby species which have been listed as characteristic of rock ravines. But along with these grow *Lycopodium obscurum*, *Oakesia sessilifolia*, *Corylus americana*, *Geranium maculatum*, *Chimaphila umbellata*, *Pyrola rotundifolia*, and *Erigeron pulchellus* —all plants of relatively dry, open woods. As might be anticipated, the bryophytic flora is poorly represented. The rock-face and crevice mosses and liverworts, which constitute such a striking feature of the vegetation in rock ravines, are absent. Along the wet, sandy banks of the stream are a few species, such as *Pellia epiphylla*, *Conocephalum conicum*, *Mnium hornum*, and *Catharinaea undulata;* but aside from these about the only bryophytes present are a few forms which grow on rotten wood or humus, such as *Mnium cuspidatum*, *Stereodon cupressiformis* and *Georgia pellucida*.

Ravines in unconsolidated rock compare neither in scenic nor botanic interest with rock ravines. To be sure, all gradations are found between extremely shallow and scarcely perceptible depressions, which ordinarily would hardly be classed as ravines, and ravines of considerable depth, with fairly steep sides, like the one at Windsor. As a result of the diversity in environments which it is obvious may thus be afforded by different ravines, all stages of transition may be found between the vegetation of swamps and uplands on the one hand and that of typical ravines on the other. On the average, however, ravines in unconsolidated

rock are smaller in size and are relatively broader and shallower than rock ravines. In consequence, the atmospheric conditions are seldom as favorable as those of rock ravines, and the vegetation rarely equals that of rock ravines in the high degree of mesophytism attained. Soil moisture, as a rule, would seem to be more important here in its effect on vegetation than atmospheric humidity. The boreal tone which characterizes the vegetation of rock ravines is likewise lacking. This would naturally be expected, not only on account of the less congenial environmental relations but also because of the comparative recency with which ravines in glacial deposits have been developed.

Spring Brooks.—As Cowles* has remarked, "springs and spring brooks may be classed with ravine streams, but differ from them in the relative absence of erosion phenomena." They might equally well, if not better, be classed with spring swamps,† with which they are usually associated. Spring brooks are common throughout Connecticut. Perhaps their most familiar floristic feature is the fringe of alders (*Alnus rugosa*, *Alnus incana*) which almost invariably lines their banks. Aside from these, the brookside flora may include any of the species elsewhere cited as characteristic of spring swamps.

The Succession of Vegetation during the Development of Ravines in Unconsolidated Rocks.—In his treatment of the plant societies of the Chicago region, Cowles‡ has described the development of clay ravines and the concomitant sequence of plant associations. The following observations are quoted from this work: "Wherever there is an elevated stretch of land adjoining a body of water, such as a lake bluff, one is apt to find excellent examples of the beginning of a ravine. *Fig. 1* [reproduced in this paper as FIG. 4] shows an embryonic ravine of a type which may frequently be seen along the clay bluffs. . . . A ravine of this type is essentially a desert, so far as plant life is concerned. The exposure to wind and to alternations of temperature and moisture is excessive. The lack of vegetation, however, is due chiefly to the instability of the soil; this instability is particularly great in the case of clay bluffs, where the seepage of water causes extensive landslide action.

* The physiographic ecology of Chicago and vicinity. Bot. Gaz. 31: 98. 1901.

† See Bull. Torrey Club 42: 192, 193. 1915.

‡ *Op. cit.*, pp. 86–88.

No plants can yet get a foothold in such a place, unless it be a few species that may be able to make their appearance between periods of landslide action; among these plants annuals particularly predominate. The perennials that may be found in such places are almost entirely plants which have slid down the bank. Ravines of a similar type may be seen in many places inland, and wherever found the poverty of vegetation on the slopes is the most striking character.

FIG. 4. An embryonic ravine in a clay bluff along the western shore of Lake Michigan. Vegetation entirely absent on the unstable clay slopes, except for shrubs and grasses which have slid down from the top. (After Cowles, Physiographic ecology of Chicago and vicinity; photograph furnished by H. C. Cowles.)

"As the ravine extends itself inland the conditions outlined above may be always seen about its head, but toward the mouth of the ravine the slopes are less precipitous. Torrents cut down the bed of the ravine until a depth is reached approaching the water level at its mouth. From this time on the slopes become reduced and the ravine widens more than it deepens, by reason of lateral cutting, landslide action, and side gullies. After a time a sufficient stability is reached to permit a considerable growth of vegetation.

If the erosion is slight enough to allow a vegetation carpet to develop, a high degree of luxuriance may be attained. In fact, ravine conditions are usually extremely favorable for plants, after the initial stages have passed. In a comparatively few years the vegetation leaps, as it were, by bounds through the herbaceous and shrubby stages into a mesophytic forest, ... Nothing shows as well as this the brief period necessary for a vegetation cycle in a favored situation as compared with an erosion cycle."

In Connecticut, clay ravines are much less frequent than are those in rock. They exist on a small scale in many parts of the Central Lowland, especially along the Connecticut River from Glastonbury to Windsor Locks, but elsewhere they are rare. Nowhere in this state are the successive changes in vegetation which accompany the development of a clay ravine so clearly shown as in the area described by Cowles, an area which the writer has visited on several occasions. So far as it has been possible to compare, however, the observations recorded in the Chicago region seem quite applicable to conditions in Connecticut.

PRE-EROSION TOPOGRAPHY AND ITS BEARING ON THE PHENOMENA OF SUCCESSION IN ROCK RAVINES

"From the standpoint of dynamic plant geography our land areas are divided into two well-marked categories: on the one hand is the erosion topography which is characteristic of the eroding and depositing phases of present streams and shores, and on the other hand is the preërosion topography which is characteristic of those areas that have not as yet been invaded by erosive forces."* To this latter category, speaking from the standpoint of the succession of plant associations, belong rock ravines. For while it is conceivable that, just as in the case of clay ravines, the topographic changes which accompany the development of rock ravines might react on the vegetation, yet such changes are brought about with such extreme slowness that their effect on plant life may be regarded as practically negligible. Whatever changes in the nature of ravine vegetation may have taken place in the past have probably been associated not only with topographic changes but with climatic changes as well; and the same will very likely

* Cowles, H. C. Bot. Gaz. 51: 172, 173. 1911.

hold true in the future. From a standpoint of present-day plant geography, therefore, the climax vegetation of rock ravines may be looked upon as practically permanent.

Although the fact cannot be overlooked that ordinarily the plant societies of rock ravines are associated with a definite phase of stream development, it should also be recognized that while very commonly the formation of a ravine has been due to the activity of streams which are still operative, this is by no means always the case. There are many rock ravines whose formation cannot be accounted for by contemporaneous factors at all. Often, as in the Devil's Gulch, the streams now present in such ravines can have played little part in their formation. Many streams have been superposed, so to speak, on the topography. They have found rather than made their channels. Not infrequently, as in the Wolf Den, ravines have been developed in other ways than by stream erosion. It is largely due to the prevalence of this preërosion type of topography, which has been moulded by physiographic forces of the geologic past, that rock ravines are so much more highly developed in the Highlands than in the Lowland.

RIVER AND STREAM BLUFFS

The later phases in river activity may be observed along most of the larger streams throughout the state. As the result of lateral cutting, the ravine once present has been replaced by a broad valley. As a ravine widens out, the exposure to wind, sun, and changes of temperature increases, and the moisture content of the slopes is appreciably modified. The effect of these environmental changes on vegetation can be seen by comparing the flora of a river valley with that of a ravine. In a general way, the vegetation of stream valleys can be treated under two heads: BLUFFS and FLOOD PLAINS. The term Bluff, as used here, includes not only the relatively steep slopes which frequently demarcate the valley from the upland, but also the gentler slopes which commonly occupy most of the intervening valley floor. In other words, it embraces all parts of the valley which, in contrast to flood plains, have been formed by erosion rather than by deposition.

The Vegetation of Bluffs in Unconsolidated Rocks.—In the

Chicago region,* the increased exposure which follows the widening out of a clay ravine may have a disastrous effect on the ravine flora.

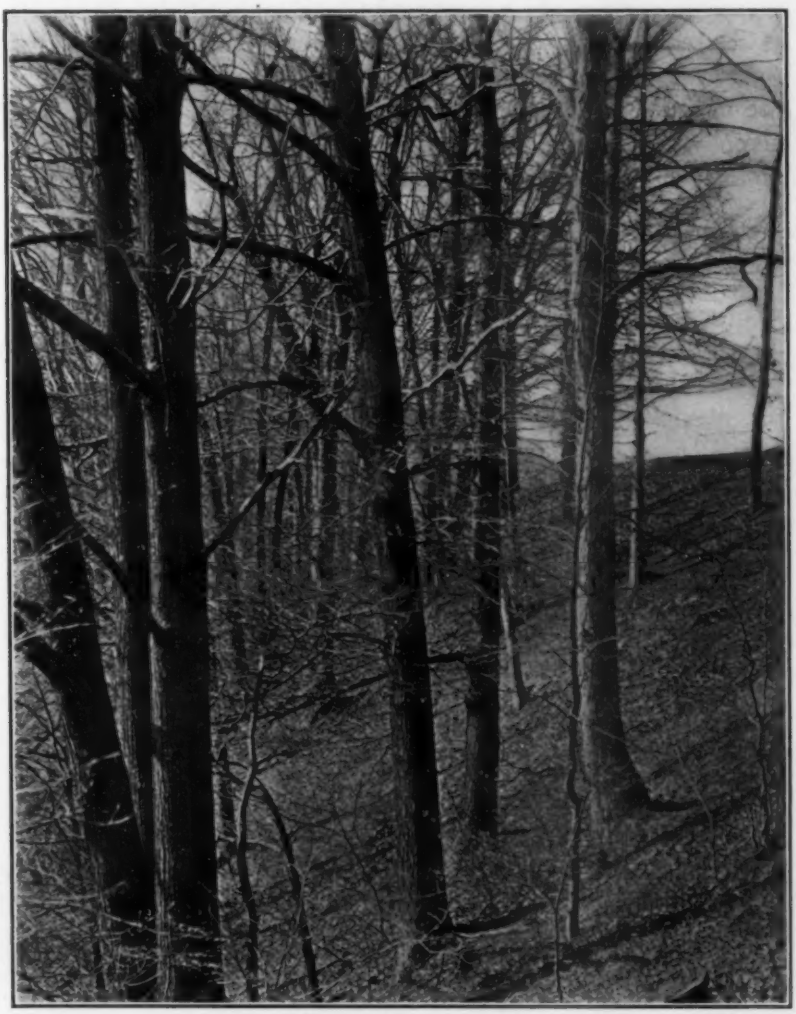


FIG. 5. Forest of chestnut, white oak, red oak, etc., along a sandy bluff bordering West River, New Haven. Elsewhere along the bluff, hemlock, beech and basswood are more or less abundant.

"The rich mesophytic herbs, including the liverworts and mosses, dry up and die, . . . and a xerophytic undergrowth comes in. . . .

* See Cowles, H. C., 1901, *op. cit.*, pp. 90–93.

After a few years have passed, xerophytic shrubs appear, . . . and it is not long until xerophytic or semi-xerophytic thickets prevail in place of the former mesophytic undershrubs. The last of the mesophytes to die are trees, because they are longer-lived than herbs and shrubs, and also because their roots reach down to the moisture"; but eventually these too give way to relatively xerophytic species. In Connecticut, the changes are not so radical; in fact, a bluff forest may be scarcely less mesophytic than a ravine forest. This is not surprising when it is considered that the climax formation in this region (that is, the most mesophytic type of vegetation which is capable of development on uplands) is very nearly as mesophytic as the climax association (termed by Cowles a "temporary climax") of ravines. In the Chicago region, on the other hand, the contrast between the mesophytic ravine forests and the xero-mesophytic climax forests on uplands is very pronounced.

The most striking difference between a bluff forest (FIG. 5) and a ravine forest is seen in the greater abundance of relatively intolerant trees. The undergrowth also, while it may contain any of the characteristic ravine species, includes many forms which ordinarily do not thrive under the shadier ravine conditions. On bluffs in unconsolidated rock, especially on clay and till, the soil moisture relations usually favor the continuance of a mesophytic flora. Near the mouth of the Windsor ravine, to select a concrete example, along the bluffs which border the Farmington Valley, common trees are *Juglans cinerea*, *Tilia americana*, *Betula alba papyrifera*, *Ulmus americana*, *Platanus occidentalis*, *Carya cordiformis*, *Quercus rubra*, *Ostrya virginiana*, and *Carpinus caroliniana*. Along with these occur the trees of the ravine forest—the sugar maple, white ash, tulip and yellow birch, and to a less extent the hemlock.

The undergrowth of moist valley forests is particularly rich in spring-flowering species. Among the herbaceous plants characteristic of such habitats may be mentioned the following:

Aspidium noveboracense	*Botrychium virginianum*
Asplenium Filix-femina	*Oakesia sessilifolia*
Adiantum pedatum	*Allium tricoccum*
Osmunda Claytoniana	*Erythronium americanum*

Asarum canadense	*Hepatica triloba*
Claytonia virginica	*Anemone quinquefolia*
Thalictrum dioicum	*Caulophyllum thalictroides*
Anemonella thalictroides	*Sanguinaria canadensis*
Smilacina racemosa	*Dicentra cucullaria*
Polygonatum biflorum	*Dentaria diphylla*
Medeola virginiana	*Dentaria laciniata*
Trillium erectum	*Viola pubescens*

The Vegetation of Rock Bluffs.—In comparing rock bluffs with rock ravines, one striking dissimilarity concerns the bryophytic flora. Species inhabiting the rock-face or the crevices, together with certain of the forest-floor species, may be well represented, but most of the others are absent. Under favorable circumstances a rock bluff may support a highly mesophytic vegetation; much apparently depends on exposure and on ground-water relations. Along the Connecticut River, south of Middletown, the north-facing bluffs are (or were) well forested; most of the vascular plants already cited as characteristic of rock ravines grow luxuriantly; *Acer pennsylvanicum* is common, attaining a height of more than thirty feet; and the mesophytic ravine mosses are well represented. The vegetation on the south-facing bluffs across the river, however, especially as regards the herbaceous flora, is much less mesophytic. In general, north- or east-facing bluffs are more mesophytic than those which face south or west. As might be expected, the highest degree of mesophytism prevails toward the bottom of a bluff; toward the top the vegetation is more xerophytic. In some cases, where the water supply is insufficient, mesophytes may be virtually lacking and xerophytes predominate from top to bottom. On the whole, the vegetation of the rock bluffs which border stream valleys throughout the state resembles that which has been described elsewhere* as characteristic of talus slopes.

FLOOD PLAINS

The topographic changes which take place during the building up of a flood-plain are accompanied by a fairly definite succession of plant associations. In the earlier stages of flood plain develop-

* See Torreya 14: 181–184. 1914.

ment, the surface of the ground is so low that it is covered with water at all seasons of the year. Here the vegetation consists of aquatic or semi-aquatic plants. As the surface is built up higher, it reaches a level where it is exposed to the air during summer, the period of low water, and here aquatic plants are replaced by terrestrial herbs. As the constructive process continues, the surface is built up to a height where it is out of water much of the year, and finally it may attain an elevation where it is out of reach of all but the highest floods. On these older flood plains grow shrubs and trees.

Flood Plain Associations along the Connecticut River.—Flood plains are formed to some extent along every sizable stream. In Connecticut, as might be expected, they are developed on the largest scale along the Connecticut River. Here, on the higher flood plains from Middletown northward, the rich alluvial soil furnishes the most fertile farm-lands in the state. As the result of agriculture, much of the primitive vegetation has been obliterated,* but it may still be seen to advantage on various flood plain islands (FIG. 6) and elsewhere. On an island at Windsor, in particular, the natural vegetation has never been disturbed. Whether or not it is true, as old residents maintain, that this island —now about three-quarters of a mile long, perhaps a hundred yards wide, and rising to a height of more than a dozen feet above low water level—has been developed entirely within the last thirty years, it is certain that it is growing rapidly at the present time, having increased several hundred feet in length at the lower end since it first came under the writer's observation in 1910. The following notes on the vegetation of the Connecticut River flood plains are based partly on the study of this island, partly on studies made at Middletown, Haddam and other points along the river.

As compared with a lake-swamp succession, free-floating aquatics, for obvious reasons, are rarely represented in a flood

* Many of the grassy meadows along the Connecticut date back to pre-colonial days. It is recorded that when the first settlers arrived these areas were open and under cultivation by the Indians, who were accustomed to burn them over annually. But from the fact that today trees occur along the sloughs and scattered through the grassland, wherever they are permitted to grow, it would seem probable that these meadows were formerly forested, and that, if left to themselves, they would soon revert to their original condition.

plain succession. The pond-lilies also are usually absent. Commonly the first forms to appear are submersed species, such as the pondweeds (*Potamogeton* sp.), *Vallisneria spiralis* and *Elodea canadensis*, which may grow in water four or even more feet in depth. In shallow water various aquatics with aerial foliage are ordinarily conspicuous. Of these, the following species are perhaps the most noteworthy:*

FIG. 6. Flood plain island in the Connecticut River, at Haddam. The plant in the foreground is the wild rice (*Zizania palustris*).

Equisetum fluviatile
Typha latifolia
Sagittaria latifolia
Zizania palustris
Scirpus americanus
Scirpus validus
Peltandra virginica
Orontium aquaticum
Pontederia cordata
Polygonum Muhlenbergii

While the number of species present at this early stage of flood plain development is relatively small, any lack of variety is more than counterbalanced by the luxuriance with which these

* From this and the two following lists have purposely been omitted a number of species which, while peculiar to the Connecticut River flood plains, seem too rare or too local to be of importance in the present connection. The majority of such species, so far as known, have already been mentioned elsewhere (Torreya 13: 106. 1913).

few forms often grow. Fringing zones of pickerel weed and the like are quite as characteristic of flood plains as of lake shores, while marshy swamps, predominated by wild rice (FIG. 7) and other grass-like plants, are a prominent feature of many low flood

FIG. 7. Wild rice along banks of the Quinnipiac River, North Haven. Some idea of the height of this grass is suggested by the bow of the canoe in the foreground.

plains, particularly toward the mouth of the river. Here, within the sphere of tidal influence, the ground occupied by these plants may be submerged at high tide and bare at low tide.

The second phase of flood plain development may well be designated the Strand Stage (FIG. 8). The surface of the ground is exposed for a longer or shorter period during summer, but is covered with water during winter. Certain algae, such as *Vaucheria* and *Botrydium*, are common here, as are also ephemeral bryophytes, such as *Riccia*, *Ephemerum*, and *Physcomitrium immersum*. The predominant vascular plants are either annuals or herbaceous perennials (or biennials)—forms which are able to develop between successive periods of submergence. On the lower, muddier parts

FIG. 8. A typical, low, flood plain strand along the Connecticut River, at East Windsor. Vegetation mostly herbaceous, but seedlings of willow and cottonwood abundant.

of the strand, species with more or less pronounced amphibious proclivities may be well represented: such, for example, as *Echinochloa Walteri*, *Eleocharis aciculare*, *Penthorum sedoides*, and *Ludvigia palustris*. A list of other species characteristic of the strand stage is here given.

Equisetum arvense
Panicum agrostoides
Leersia virginica
Cyperus strigosus
Juncus effusus
Rumex crispus
Polygonum pennsylvanicum
Radicula palustris
Gnaphalium uliginosum
Ambrosia trifida
Xanthium echinatum
Bidens vulgatum

Woody plants are seldom wholly absent from the strand stage of a flood plain; commonly, seedlings of willow and cottonwood are abundant. Indeed, certain species of willow, such as *Salix cordata* and *Salix longifolia*, occur here which are usually lacking on older flood plains. But woody plants are rarely well developed; for even if they are able to withstand submergence in winter, trees and shrubs of any size are liable to be badly battered or else

FIG. 9. Nearly pure growth of willow (*Salix nigra*) near southern extremity of flood plain island in Connecticut River, Windsor.

uprooted and carried away by the ice when it breaks up in spring. As soon, however, as the surface has been built up to such a height that it is beyond the reach of the winter ice, trees become the controlling element of the vegetation and ultimately a luxuriant forest may be developed. The boundary between the wooded part of a flood plain and the strand area is often marked by a distinct shelf or step—the result of ice-shove in winter.

One of the first trees to establish itself on the flood plain is the black willow (*Salix nigra*). The willow is essentially a pioneer. Young flood plain forests (FIG. 9) may be composed almost wholly of this tree, while a zone of willow almost invariably fringes the shoreward margin of older forests. Closely following the willow, in fact often appearing simultaneously with it, are other trees, such as the sycamore (*Platanus occidentalis*) and the cottonwood

FIG. 10. Cottonwood forest with luxuriant herbaceous undergrowth (*Laportea*, etc.) on flood plain island at Windsor.

(*Populus deltoides*), particularly the latter. As the surface of the ground continues to be built up higher, the soil becomes relatively drier and better aerated, so that conditions rapidly become less hydrophytic and more mesophytic. Under the changing conditions of soil and light, the willow gradually assumes a position of less and less importance, while the cottonwood comes to occupy a more and more prominent place in the rising forest (FIG. 10).

For while, like the willow, the cottonwood is relatively intolerant of shade, it grows more rapidly and to a much larger size, so that it tends to overtop and shade out the willow. Meanwhile other trees make their appearance. In addition to the species already enumerated, common trees on the Connecticut River flood plains are the elm (*Ulmus americana*), silver maple (*Acer saccharinum*), basswood (*Tilia americana*), white ash (*Fraxinus americana*) and red ash (*Fraxinus pennsylvanica*). Without exception, all of these last-named trees are more tolerant of shade than their predecessors. Springing up in the light shade which the cottonwood and willow produce, these more tolerant species become increasingly abundant until ultimately they dominate the forest. And while today the cottonwood and willow are perhaps the most conspicuous trees of the Connecticut River flood plains, there is little doubt that the forests which originally clothed the higher flood plains were made up largely of elm, silver maple, basswood, and ash.

A striking feature of the vegetation in flood plain forests is the wealth of lianas. Woody forms, such as *Rhus Toxicodendron*, *Vitis vulpina*, and *Psedera quinquefolia*, ascend the trunks of trees and hang in graceful festoons from the branches. A few herbaceous lianas also, notably *Sicyos angulatus* and *Echinocystis lobata*, clamber the trees, while numerous less vigorous species, *e.g.* *Polygonum scandens*, *Amphicarpa monoica*, *Convolvulus sepium*, *Solanum Dulcamara*, and *Clematis virginiana*, twine about or cling to any available support. The parasitic *Cuscuta obtusiflora* is a common form on the Windsor flood plain. Shrubs are usually few and scattered, about the only forms ordinarily present being *Cornus Amomum* and *Sambucus canadensis*.

The herbaceous undergrowth in such a forest is rank and luxuriant; some idea of its character is conveyed by FIG. 10. Tall, broad-, thin-leaved mesophytic plants predominate. The giant ragweed (*Ambrosia trifida*) commonly reaches a height of from ten to twelve feet, and the ostrich fern (*Onoclea Struthiopteris*), largest of the native ferns, a height of more than six feet. The nettles (*Laportea canadensis* and species of *Urtica*), growing more than waist-high, are uncomfortably abundant. Other characteristic herbaceous species worthy of mention are the following:

Asplenium Filix-femina
Onoclea sensibilis
Leersia virginica
Muhlenbergia mexicana
Cinna arundinacea
Bromus altissimus
Elymus canadensis
Pilea pumila
Boehmeria cylindrica
Thalictrum polygamum
Impatiens biflora
Viola cucullata
Circaea lutetiana
Verbena hastata
Eupatorium purpureum
Eupatorium urticaefolium
Solidago serotina
Aster paniculatus
Helenium autumnale

Flood Plain Associations along Other Streams.—The conditions described in the preceding paragraphs are found not only along the Connecticut, but also along the Housatonic and to a considerable

FIG. 11. Cat-tail (*Typha latifolia*) marsh along Muddy River, North Haven. In the background is a flood plain forest of elm, pin oak, etc.

extent along others of the larger rivers. But even along these rivers, there is a more or less noticeable variation in the aspect of flood plain associations, while along the smaller streams the departure from the described conditions may be very pronounced. On gravelly or stony flood plains, such as occur along swift streams, the pioneer forms of vegetation may be scraggly willows, alders,

and red-osier dogwood, along with which may grow a few herbaceous plants. Along many of the smaller streams throughout the state, during the building up of a flood plain, a sequence of plant associations is commonly encountered which is essentially similar to what has been described in an earlier paper* as characteristic of lakes and swamps. With the exception of the free-floating forms, any of the aquatic plants there mentioned may occur here. Of the species with aerial photosynthetic organs, the cat-tail (*Typha latifolia*) is especially conspicuous along many slow streams, frequently monopolizing wet, swampy tracts to the exclusion of practically everything else (FIG. 11). Marshes and meadows are quite as frequently developed along streams as along lake margins, and in general the aspect of the vegetation is similar in either case.† *Phalaris arundinacea* and *Leersia oryzoides*, however, might be mentioned as being more common in alluvial swamps than in other habitats. All of the shrubs and trees listed as characteristic of lake swamps are likewise found on flood plains along streams. Typical flood plain forests are best developed in areas which are subject to inundation only in spring. Here the soil relations are essentially those of a periodic swamp. Prominent trees in these forests along most streams are *Quercus bicolor* and *Quercus palustris*, species which are at least very infrequent in similar situations along the Connecticut. Except along the larger rivers, on the other hand, the cottonwood is practically absent and the silver maple is scarce. In addition to the two oaks already mentioned, the following trees are commonly represented in flood plain forests.

Carya cordifolia	*Acer rubrum*
Carpinus caroliniana	*Tilia americana*
Ulmus americana	*Nyssa sylvatica*
Liriodendron tulipifera	*Platanus occidentalis*

* Bull. Torrey Club 42: 176–194. 1915.

† Regarding the vegetation of Connecticut meadows in general it should be remarked here that while in the case of many wet meadows there seems to be no doubt that the present vegetation represents the original type, this is probably not true of all present-day meadow-lands. There is reason to believe that most of the less wet areas now occupied by meadow associations were formerly forested, and that their present vegetation has been developed only as a result of human interference with the original conditions. See footnote on p. 254.

Fraxinus americana *Fraxinus pennsylvanica*
Fraxinus nigra

The Temporary Nature of Flood Plain Forests.—It has been shown in the preceding pages that during the development of a flood plain the vegetation becomes less hydrophytic and more mesophytic, culminating in the formation of a mesophytic forest. Such a forest is to be regarded as the climax association of flood plains. But it can easily be seen that, owing to the activity of the river, this forest may be relatively short lived; in other words, it may represent only a temporary climax. For as the river meanders about on its flood plain in serpentine curves, it is constantly wearing away its banks on the outer, concave side of each bend, while at the same time deposition is usually taking place on the opposite, convex shores. In this way "a river may swing quite across its flood plain, destroying all that it has built, including the mesophytic forest."* Changes of this sort take place with appreciable speed and may be observed along almost any depositing stream.

Ox-bow Ponds.—In this connection should also be mentioned the crescent-shaped curves, or ox-bows, which are a characteristic feature of old-age streams. Frequently the meandering river shifts its course, abandoning a loop-like channel for a more direct route. The loop then becomes an ox-bow pond (FIG. 1, D), and as such its vegetation can best be treated with that of ponds and swamps.†

The Subsequent History of Flood Plains.—One other phase of river activity may be briefly sketched. It has already been shown that while deposition is the main feature of old-age streams, erosion is not wholly absent. In the course of time, for various causes, downward cutting may be renewed, the flood plains become terraces, and new flood plains may ultimately be formed at lower levels. The resultant topography is well illustrated along the Connecticut and others of the larger streams. The low flood plains of today are comparatively recent in origin. The more ancient flood plains are represented by sandy terraces, of which

* Cowles, H. C., 1901, *op. cit.*, p. 107.

† See Bull. Torrey Club 42: 171. 1915. *Fig. 1* of this paper pictures a typical ox-bow pond.

there may be one or more. These have attained their present condition through the downcutting of the rivers into the deep fill of glacial drift and outwash.* The effect of the changed topographic relations on these former flood plains as habitats for plants is readily comprehended. With the lowering of the river they must gradually have become more and more xerophytic and thus less and less tenable for the flood plain mesophytes. The actual effect of these changes on vegetation can only be conjectured. For, just as has been pointed out in the case of rock ravines, the period of time involved has been so great that oscillations in climate as well as changes in topography must presumably be taken into account. At the present day the vegetation of river and stream terraces is perhaps best treated with that of uplands, since the river has long since ceased to act as a dynamic factor in its development.

ACKNOWLEDGMENTS

For suggestions in connection with the preparation of this paper, the writer is greatly indebted to Professor Joseph Barrell, of the Geological Faculty, and Professor A. W. Evans, of the Botanical Faculty of Yale University, and to Mr. C. A. Weatherby, of East Hartford.

SHEFFIELD SCIENTIFIC SCHOOL OF YALE UNIVERSITY

* In this connection, see Rice, W. N., & Gregory, H. E., Manual of the Geology of Connecticut. Conn. State Geol. and Nat. Hist. Surv. Bull. 6: 35, 36. 1906.

The ferns and flowering plants of Nantucket—XVII

EUGENE P. BICKNELL

COMPOSITAE—*continued*

BACCHARIS HALIMIFOLIA L.

Very local, and confined to the eastern side of the island. As long ago as 1849 it was rather numerous on Coskaty, according to Mrs. Owen, and it is abundant there today. It occurs also on Coatue, and extends sparingly from Polpis southeasterly towards Siasconset, well away from any direct saline influence. A single small plant was seen in one of the higher bogs on Saul's Hills, and a shrub nearly seven feet tall in Gibb's Swamp. In 1904 a large clump grew in dry open ground about a mile northwest of Siasconset. Not yet in bloom September 6, 1904; in full flower September 17, 1899.

PLUCHEA CAMPHORATA (L.) DC.

Common about pools and mud flats in tidal marshes, blooming in August and September.

ANTENNARIA PLANTAGINIFOLIA (L.) Richards.

Found everywhere throughout the island, along roadsides, on banks and in pine groves, in damp meadows with *A. neglecta* and on dry hills with *A. neodioica*, on the plains and commons and on dry lichen-clothed levels in the poorest soils. In full flower May 31, 1909, except in the shade of pines where only the most forward plants were in bloom; mostly gone to seed by June 15, 1910.

Exceedingly variable, forms with broad rounded leaves, and forms with narrowly oblanceolate leaves on elongated petioles (var. *petiolata* Fernald) often growing side by side. A small form having narrow and acute leaves, collected in the Miacomet pines, is especially noteworthy by reason of reddish glandular hairs scattered along the stems, these being rather numerous in some examples. More noteworthy still is a very small form found also among the Miacomet pines. It is at once set apart from

reduced examples of true *A. plantaginifolia* by perfectly white instead of purple styles, and is further well characterized by very small, orbicular to obovate, short-petioled basal leaves, often in a close rosette, their blades only 0.75–1.5 cm. broad; the cauline leaves are mostly blunt or rounded at the apex, their upper surface invested with a minute appressed tomentum quite different from the loosely arachnoid pubescence characteristic of the attenuate-tipped cauline leaves of true *A. plantaginifolia*. Not any of the pistillate plants were taller than 10–15 cm., and the few staminate plants found were only 3–5 cm. high; in several of them a few of the involucral bracts were bright rose color. Altogether the plant possesses a combination of striking characters that give it quite the aspect of a most distinct species. But certain Nantucket specimens of *A. plantaginifolia* show a tendency to develop somewhat similar characters, thus making it doubtful whether the smaller plant is other than a localized variety of the common species.

*ANTENNARIA FALLAX Greene.

On Prospect Hill in the western outskirts of the town, also on a dry slope at Capaum Pond, only a few plants at each station. In full flower June 10, 1909; flowers passing, June 5, 1911. A stout form of the species, becoming 4 dm. high, the acute leaves 2–3 cm. broad, pubescent on the upper surface; some stems with a few purplish glandular hairs below the rather close corymb.

*ANTENNARIA NEODIOICA Greene.

Rather common locally, but wanting in many parts of the island; perhaps most frequent on the rolling commons westward from the town; Madequet, Shawkemo, Siasconset. In full bloom, but also much of it only just in flower May 30, 1909, some heads mature by June 6.

Much of the Nantucket plant appeared to be somewhat aberrant, and specimens sent to Professor Fernald proved to be his var. *attenuata* (Proc. Bost. Soc. Nat. Hist. **28**: 245. 1898). My collections seem to show that this variety is more common on Nantucket than the typical plant. Professor Fernald writes me that it appears to be more common than the type in the Canadian zone.

*ANTENNARIA NEGLECTA Greene.

In damp fields and open places, rather scarce and found mainly on the western side of the island. In full flower May 31, 1909; mature heads June 7, 1908.

*ANTENNARIA PETALOIDEA Fernald.

An extensive colony of this interesting plant overspreads many rods of a sterile hilltop field southwest of Capaum Pond, an extreme southern outpost of the species. On May 30, 1909, in fullest bloom, it was far more conspicuous in the whiteness of its inflorescence than any of our more familiar Antennarias, appearing like snow drifted along the hilltop with outlying patches down the slope. I had never before met with the species nor understood just how it differed from *A. neglecta*, but the eye needed no closer inquiry to approve it instantly as a beautifully distinct plant. Professor Fernald, who has kindly examined my specimens, writes me that they are typical of his var. *subcorymbosa* (Rhodora **16**: 133. 1914) not known hitherto from south of Mt. Desert, whence it extends locally along the coast to Prince Edward's Island and eastern Nova Scotia, there very common, and further eastward to Newfoundland.

ANAPHALIS MARGARITACEA (L.) Benth. & Hook.

Not an abundant plant, but widely scattered over the island. It is frequent in close patches among the mixed growths of herbs and low woody plants that like miniature thickets are scattered over the plains and rolling upland, and is common in more open colonies on parts of Great Neck. Corymbs white, but no open flowers, July 10, 1912; in full flower through August and September.

The close groups or patches, often far distant from each other, that are natural to its habit of growth in poor soils, are noticeable early in the season before the stems appear, from the whitish green color of the basal leaves; by midsummer it has become a conspicuous plant from the snowy whiteness of its flowering corymbs.

GNAPHALIUM OBTUSIFOLIUM L.

Common in dry soils, often in white sand among the beech grass. Plants very small up to late June; in full flower in August and September.

GNAPHALIUM ULIGINOSUM L.

Locally common in damp fields and cartways and occasional in the town streets. First flowers June 17, 1910; blooming through September.

GNAPHALIUM PURPUREUM L.

On sandy levels about most of the ponds along the south side of the island, especially Nobadeer and Madequecham Ponds, sometimes in great abundance. Collected by Miss Gardner at Sachacha Pond. Reddened flower heads June 7, 1909; plants still small but in full flower July 9, 1912; flowers passing September 13, 1907.

*INULA HELENIUM L.

Sparingly established in a meadow near the Springfield House and in a low field at the southern end of the town. In full flower August 4, 1906; out of bloom August 27, 1904.

RUDBECKIA HIRTA L.

Frequent or rather common in many parts of the island. According to Mrs. Owen its first appearance on Nantucket was probably about 1878 and ten years later it was rather common at Siasconset and becoming so elsewhere.

HELIANTHUS DIVARICATUS L.

Common on the plains and moorland towards Siasconset, and local throughout the eastern third of the island, not seen on the western two thirds. In exposed places on poor soils it is often much dwarfed, with unusually narrow leaves and few flowering heads or only a single one. In full bloom August 6, 1904; mostly passed flowering September 17, 1907.

HELIANTHUS STRUMOSUS L.

Locally common in the northeastern quarter of the island in dry soil about the borders of thickets; not seen west of Swain's Neck. No flowers up to August 3, 1906; in full bloom September 17, 1907.

*HELIANTHUS ANNUUS L.

Occasional in waste ground and in old fields. In full flower August 11, 1906.

*HELIANTHUS SCABERRIMUS Ell.

A casual waif. A single small flowering plant in an old field September 15, 1899; one plant past flowering September 20, 1907, in waste spot west of the town; a few small plants near Crooked Lane June, 1908.

HELIANTHUS TUBEROSUS L.

Yards and waste places and by roadsides, mainly near the town, growing in close colonies and not coming into full bloom until late in the season. Plants a few inches high June 3, 1909; a precocious flowering head September 11, 1904; earliest flower September 14, 1907.

BIDENS CERNUA L.

Frequent in wet places and locally abundant, as at Watt's Run and along ditches west of the town. Just in flower August 30, 1904; in full bloom September 14, 1907. Stout forms, having closely serrate leaves becoming 4 cm. broad, correspond with specimens in the herbarium of the New York Botanical Garden labeled var. *elliptica* by Dr. Wiegand (Bull. Torr. Club, **26**: 417–418).

BIDENS CONNATA Muhl.

Everywhere in low grounds, in bogs and along pond shores. At Maxcy's Pond five feet tall, with leaves as deeply lobed as in the smaller forms. No flowers up to August 15, 1906; just in flower at the end of August, 1904; blooming through September.

*BIDENS PETIOLATA Nutt.

Collected only in low grounds west of the town. Freshly in bloom September 21, 1899.

A plant of wet woods and thickets rather than of open bogs, and apparently not a common species on the immediate coast. I used to find it an abundant and characteristic plant of low open woods and shaded swamps in the lower Hudson River region where *Bidens connata* was of such rarity, if it occurred at all, that I never met with it. When first coming to know this plant in its coastal bogs I could not doubt that it was distinct from the Hudson Valley species, and my observation of the two plants for many years has only confirmed that view.

*BIDENS FRONDOSA L.

Frequent in low grounds and waste places about the town; sometimes on pond shores. In early flower at the end of August, 1904; in full flower September 10, 1907.

*BIDENS VULGATA Greene.

Frequent in yards and waste places and by streetsides in the town; Shawkemo. Just in flower in early September, 1904; in full flower September 16, 1907.

***Galinsoga aristulata** sp. nov.

Galinsoga parviflora var. *hispida* DC. not *G. hispida* Benth.

A few plants on Easton Street in full flower September 13, 1907; Fair Street, September 19, 1914; specimen in herbarium of Miss Grace B. Gardner.

This now widespread weed wherever I have met with it has not failed to prove itself always readily distinguishable from the true *G. parviflora* Cav., even without reference to the constant and pronounced differences in the pappus scales. Nevertheless I do not discover that it has ever received an available specific name. In some European gardens of today it is evidently known as *G. brachystephana* Regel, since it has been grown at the New York Botanical Garden from seeds received from Europe under that name. There are before me specimens raised from such seeds that, noting their similarity to our plant known as *G. parviflora* var. *hispida*, I took from the herbaceous beds at the garden September 11, 1898. Although the close counterpart of these specimens has not been found in any example of our common weed met with since that time their divergencies, however obvious, are not greater than might well be expected to mark a long established garden form of so variable a plant. In any case, however, there need be no doubt that the name *G. brachystephana* in its use for this plant has been mistakenly applied. I have not been able to consult the rare pamphlet (Ind. Sem. Hort. Turic, 1846) that contains the original description of *G. brachystephana*, which species, if we may so understand its history, came from seeds received in Europe about the year 1846, from what country does not appear. Nor do I find any descriptive text in the different issues of that period of In-

dex Seminum Hortus Botanicus Imperialis Petropolitanus wherein the name appears. But a description, presumably a transcript of the original, is found in Walper's Repertorium (6: 722. 1846–7). Therein we read, "*ligulae amoene roseae.*" The correlation is thus evidently with *G. caracasana* (DC.) Sch. Bip. and not with our white-rayed species. Another name requiring to be considered is *Wiborgia urticaefolia* H. B. K. (*G. urticaefolia* Benth.). An excellent illustration of this plant accompanying its description (Nov. Gen. et Sp. 4: 257. *pl. 389.* 1820) shows that it is closely related to our species but differs by larger rays and the absence of a pappus. *G. Humboldtii* Heiron. (Bot. Jahrb. 28: 618. 1899–1900) based on a variety of *G. urticaefolia*, which is cited as a synonym, differs in having a short coroniform pappus, thus excluding our plant with elongated attenuate or aristulate pappus scales. In some respects the characterization of *G. quadriradiata* Ruiz & Pav. (Syst. Veg. 198. 1798) might seem to refer to our plant but, as a whole, it is more descriptive of, and clearly applicable to, a mere form of *G. parviflora* Cav. (*G. quinquiradiata* Ruiz & Pav. *l. c.*), as was long ago determined by De Candolle.

ACHILLEA MILLEFOLIUM L.

Fields and roadsides, flowering from early June until October. In its best developed state it is often only slightly pubescent, and is branched above the middle to form an ample compound corymb, the heads having rays 2.5–3.5 mm. broad. Reduced and more pubescent forms of poorer soils have more contracted leaves and are unbranched, bearing a single terminal corymb of somewhat smaller heads.

Dr. Rydberg, who has examined my Nantucket collections of *Achillea*, finds that certain specimens are quite clearly referable to the plant recognized in Europe as *A. asplenifolia* Vent. (*A. rosea* Desf.), in which the flowers are prevailingly rose color to magenta, and the ultimate subdivisions of the leaves finally thickened and callous at the ends below the cartilaginous pointed tip. The status of this plant, however, seems not to be very clear, and the question of its formal recognition may well await a better understanding of its relationship to *A. Millefolium*.

*ACHILLEA OCCIDENTALE Raf.

Specimens of this have been determined by Dr. Rydberg who

points out to me that its more obvious differences from *A. Millefolium* are smaller rays, 1.5–2 mm. wide, more delicately dissected leaves with narrower unmargined or but slightly margined midrib, and more arachnoid pubescence, the crowded heads commonly with more cylindric involucres and narrower and paler or more stramineous bracts. This yarrow seems to be not uncommon on Martha's Vineyard, where I have collected very typical examples, and also on Long Island and near New York. When last on Nantucket I did not well enough distinguish it from *A. Millefolium* to learn its real status there, although noting that a yarrow having very small rays, now presumably this, was not at all an uncommon plant.

*ACHILLEA PANNONICA Scheele, Linnaea **18**: 471. 1835.

A. lanata Spreng, Cat. Fl. Hal. 1799, not Lam. 1778.

This yarrow of southeastern Europe, not before, I think, reported from America, occurs in scattered growth on the dry plains towards the south shore of Nantucket especially near Madequecham Pond. In full flower July 9, 1912.

A very distinct appearing plant as compared with our common forms, densely white woolly throughout and with congested rounded or convex corymbs, and small rays 1–1.5 mm. wide. The numerous densely lanose-pubescent cauline leaves are narrow and ascending or erect, their short segments and subdivisions more or less incurved and closely crowded together. Dr. Rydberg, who has determined the identity of my specimens, has called my attention to the marked characters by which this plant differs from *A. lanulosa* Nutt. which in some respects it resembles.

ANTHEMIS COTULA L.

Mainly in and about the town and suburbs, but also in fields and waste places. A precocious flower June 18, 1910; first flowers June 27, 1912; blooming until late autumn.

CHRYSANTHEMUM LEUCANTHEMUM L.

Abundant throughout the island, whitening the fields in June. Sometimes growing in close groups in pure sand among the beach grass. First flowers May 30, 1909; in full flower June 7, 1908. All presumably the var. *pinnatifidum* Lecoq & Lamotte.

CHRYSANTHEMUM PARTHENIUM (L.) Pers.

Occasionally spontaneous by streetsides and in waste places. Not yet in flower June 14, 1908; in full flower June 27, 1912.

The more common form of this plant seen in old gardens and as an escape, has a broad pale yellow disk and short rays and would appear to be the var. *breviradiatum* Rouy (Fl. de France **8**: 263). On this understanding the less usual plant, with us, having a smaller bright yellow disk and longer rays would be the typical form. This was found growing sparingly in a barnyard west of the town in full flower September 17, 1899, and in two instances by streetsides in the town.

*CHRYSANTHEMUM BALSAMITA L.

A casual estray from cultivation, and at a few stations persistent and spreading in abandoned grounds. Large flower heads August 29, 1904; heads yellow but not actually in flower September 11, 1907.

TANACETUM VULGARE L.

Frequent near old barns and farm houses and in abandoned grounds usually growing in close masses and appearing as if a survival of cultivation. The var. *crispum* DC. is perhaps more frequent than the typical form. Begins to bloom in August and continues in full flower through September.

ARTEMISIA CAUDATA Michx.

A characteristic plant of the commons and open sandy places and often growing in pure sand among the beach grass. No heads visible June 27, 1910; inflorescence appearing June 20, 1908; not quite in bloom July 13, 1912.

ARTEMISIA VULGARIS L.

An infrequent weed, seen only about the wharves. In full flower September 5, 1904.

*ARTEMISIA BIENNIS Willd.

A single stout plant near the wharves just in flower September 5, 1904; one plant back of the beach at Wauwinet, June 20, 1910, the heads very immature.

*ARTEMISIA ANNUA L.

Collected near the Springfield House in 1901 and, more recently west of the town, by Mrs. Flynn; Main Street, September 14, 1914, Walter Burdick, specimen in herbarium of Miss Gardner.

*ARTEMISIA ABSINTHIUM L.

In full flower about a remote abandoned dwelling in Squam September 1, 1904; streetside in the town 1912.

*ARTEMISIA PONTICA L.

Casually persistent and spreading as a survival of cultivation, not seen in flower. It is more frequent on Martha's Vineyard, but only as a relic or an estray from old gardens.

*ARTEMISIA STELLERIANA Bess.

A characteristic plant of the sea beaches, mainly on the north side of the island, growing in dense confluent patches on the white sand beyond the reach of the tides; rarely seen away from the immediate shore, but becoming established in spots among the beach grass above the highest bluffs. Nearly in flower May 30, 1909, June 7, 1911; earliest flowers June 17, 1910; past its height of bloom June 27, 1912; continuing to produce some flowering stems during the summer and sometimes into September.

ERECHTITES HIERACIFOLIA (L.) Raf.

Very common, especially among the open groups of mixed woody and herbaceous vegetation that are scattered over the plains, this being the first predominating plant that springs up after these growths have been laid waste by fires. It is even more abundant among the windrows of shore refuse back of the beaches around Sachacha Pond where it becomes unusually stout and hairy and develops much purplish coloring in its upper parts. Plants a few inches high June 19, 1910, June 27, 1912; in full flower during September.

SENECIO VULGARIS L.

Streets and alleys in the town and outlying waste places, also in cultivated fields at the Cabot farm in Shimmo and on the Appleton farm at Miacomet Pond. Mature seeding heads before the end of May, but continuing to bloom throughout the season, doubtless until frost.

ARCTIUM MINUS Schk.

Infrequent; neglected places and about farm buildings near the town; Quaise; Shawkemo; Great Neck. Blooms from August through September.

*ARCTIUM TOMENTOSUM (Lam.) Schk.

The common burdock of Nantucket, inhabiting barnyards and waste places all over the island. Often with very large cottony heads and otherwise strongly typical but sometimes with the heads smaller and only thinly arachnoid, more like those of *A. minus*. Occasional forms appear to approach *A. Lappa* L. which has not yet been detected on the island. In bloom from August through September.

CIRSIUM LANCEOLATUM (L.) Hill.

Roadsides and open places in all parts of the island but nowhere in abundance. Basal leaves only June 15, 1910; first flower July 14, 1912; blooming through September.

CIRSIUM DISCOLOR (Muhl.) Spreng.

Locally common in the northeastern quarter of the island from Shawkemo to Polpis, Pocomo and, especially, in Squam. Most frequent about thickets near the shore. Comes into bloom the latest of the thistles. First flowers September 11, 1907.

CIRSIUM ODORATUM (Muhl.) Britton.

Along roadsides, and widely scattered over the downs and commons. It is often strongly developed, and plants were observed bearing as many as nine flowering heads besides several not yet in bloom. First flowers June 20, 1910, June 27, 1912; mostly past flowering in August, but flowering heads are not unusual late in the month and even in September. Heads of palest pink are frequent; occasionally they are pure white.

CIRSIUM HORRIDULUM Michx.

Common, mainly in brackish soil or in low grounds near the shore, but found as well in damp places in all parts of the island, and not infrequently in dry sandy soil, even among open growths of pine. The flowering heads, normally of a yellowish color, are often deep reddish purple medially or, rarely, throughout. First flowers June 2, 1909, June 7, 1908, June 7, 1911; some plants past flowering by June 25, 1910; mostly out of bloom by the middle of July or earlier; rarely a flowering head is produced in September.

CIRSIUM ARVENSE (L.) Scop.

Frequent near the town, and occasional elsewhere, but not much of it anywhere. First flowers July 1, 1912.

*CENTAUREA CYANUS L.

Transient in and near the town. First flowers on strayed plants June 6, 1911, June 21, 1910; flowering earlier in gardens.

*CENTAUREA MELITENSIS L.

Waste ground near Surfside, July 9, 1912, a few plants in earliest flower.

During the publication of this series further exploration on Nantucket, both by myself and by others, has brought to light a considerable number of plants not before discovered there. These later additions to the flora will be recorded in an appendix.

INDEX TO AMERICAN BOTANICAL LITERATURE

1909-1916

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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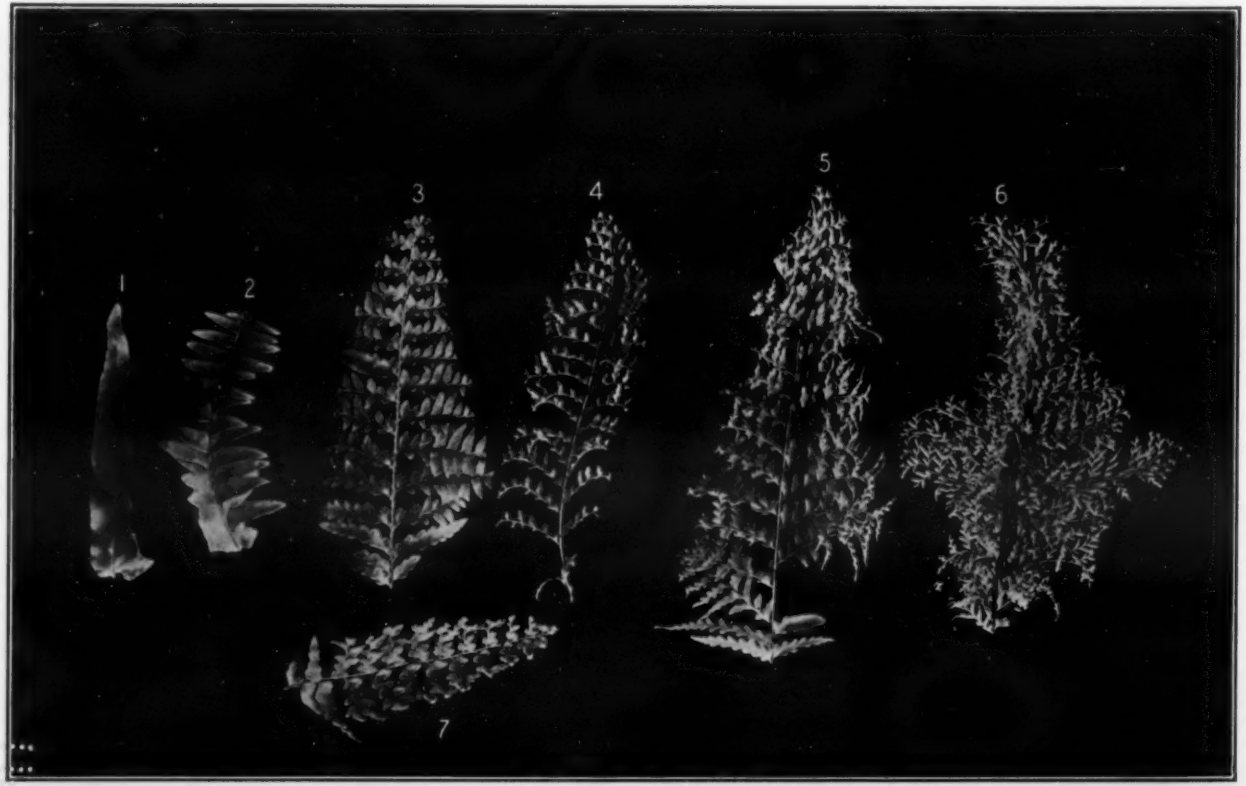

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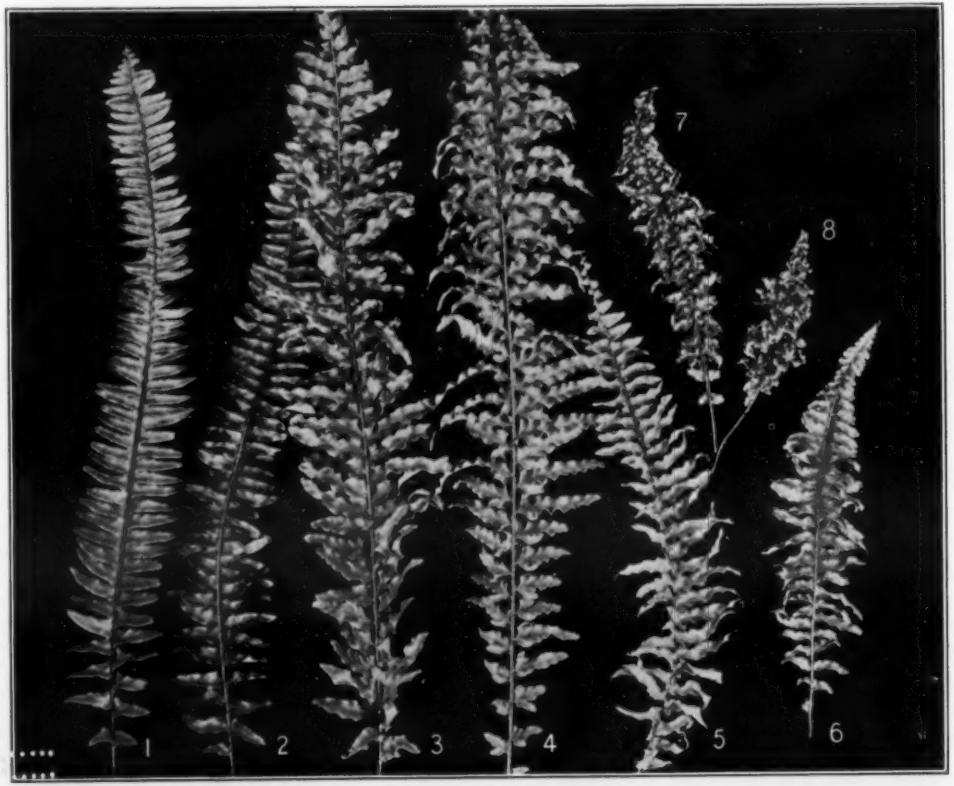

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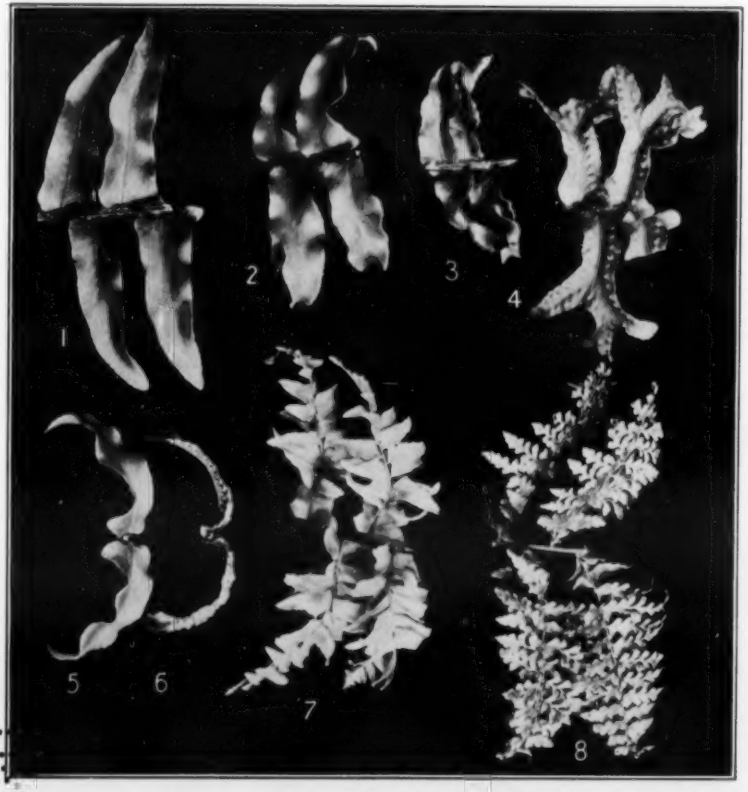

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